THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR ... Randolph Sidney Currah

TITLE OF THESIS ... The Taxonomy of Fomes roseus (Alb. & Schw. ex Fries) Cooke and Fomes cajanderi Karst.

DEGREE FOR WHICH THESIS WAS PRESENTED ... Master of Science

YEAR THIS DEGREE GRANTED ... 1979

THE UNIVERSITY OF ALBERTA

THE TAXONOMY OF *FOMES ROSEUS* (ALB. & SCHW. EX FRIES) COOKE AND *FOMES CAJANDERI* KARST.

by

© RANDOLPH SIDNEY CURRAH

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

MYCOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

SPRING, 1979

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "The taxonomy of *Fomes roseus* (Alb. & Schw. *ex* Fries) Cooke and *Fomes cajanderi* Karst." submitted by Randolph Sidney Currah in partial fulfilment of the requirements for the degree of Master of Science in Mycology.

ABSTRACT

Fomes roseus (Alb. & Schw. *ex* Fries) Cooke and *Fomes cajanderi* Karst. are wood-rotting fungi frequently found in Alberta, producing a dry, brown, cubical rot of coniferous wood. Conflicting statements in the literature concerning the specific characteristics and identity of *Fomes roseus* and *Fomes cajanderi* are the result of wide variation in the form of the basidiocarp in nature. Traditional morphological criteria fail to accurately distinguish between these species. Studies of development and hyphal anatomy of the basidiocarp indicate that differences between morphologically typical specimens of each taxon are based on a common and fundamental hyphal organization. Differences between the size of the basidiospores of each taxon are not statistically significant.

Studies of the development and morphology of isolates of *Fomes roseus* and *Fomes cajanderi* in agar and wood culture do not support the distinctions previously reported for these taxa. Growth rates of vegetative mycelium on agar indicate that variability of this feature is too great to be of taxonomic value.

Two partially characterized phenolic compounds and three benzotropolones isolated from *Fomes roseus* and *Fomes cajanderi* indicate that these species are more closely related to each other than to the type species of the genera in which they have at times been placed.

It is concluded that similarities between these species

are sufficient for placing them in one taxon under the epithet *Fomes roseus* (Alb. & Schw. *ex* Fries) Cooke. A specific circumscription is provided.

ACKNOWLEDGEMENTS

I wish to give my appreciation to Dr. L.L. Kennedy for her supervision during the preparation of this thesis. Thanks also to Dr. K.E. Denford for his helpful suggestions concerning the chemotaxonomic aspects of this work.

To Dr. Y. Hiratsuka, a note of gratitude for unlimited use of his laboratory and the Herbarium of the Northern Forestry Research Centre, Edmonton. My thanks also go to the Plant Research Institute, Ottawa for supplying herbarium material and cultures, and to the Cryptogamic Herbarium of the University of Toronto for the loan of herbarium material.

I would like to thank Ichiko Tsuneda and Carolyn Strand for their technical assistance and Louise Abele for the collection of research materials.

Finally, I express my sincerest appreciation to my wife for her unfailing encouragement throughout this work and her care in typing this thesis.

I acknowledge financial support provided by a Graduate Teaching Assistantship for two years from the Department of Botany.

TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

Wood-rotting fungi play an ecologically important role by causing the decay of wood and thus promoting the cycling of elements otherwise held in an inert and unavailable form. The majority of these fungi belong to a large and diverse family, the Polyporaceae which are characterized by producing basidia on the inside of tubes lining the undersurface of bracket-like fructifications. The basidiocarp of most species exhibits a great degree of phenotypic plasticity and consequently, since this structure has traditionally been the main source of taxonomic information, the classification of the group is decidedly artificial and highly unstable. Teixeira (1962) presents a review of the many systems of classification which have been proposed for the Polyporaceae.

Fomes roseus (Alb. & Schw. ex Fries) Cooke and Fomes cajanderi Karst. are species belonging to the family Polyporaceae. Conflicting statements in the literature concerning the specific characteristics and identity of Fomes roseus and Fomes cajanderi are the result of wide variation in the form of the basidiocarp of each species in nature.

Overholts (1953) notes that Fomes roseus and Fomes cajanderi (Fomes subroseus) have been too much confused in the literature to permit reliable conclusions regarding their specific pathological and decay characteristics. A survey of the disease and decay reports for these taxa supports this statement. Fomes roseus causes a top rot in Douglas fir (Boyce, 1923) and a decay of Thuja (Von Schrenk, 1900). Adams and Roth (1969) state that the principal heart rot fungus attacking damaged Douglas fir is Fomes cajanderi. Zeller (1926) describes a pocket rot

of stone-fruit trees produced by Fomes cajanderi which is similar to that reported by Von Schrenk (1900). Korstaian and Brush (1939) have determined Fomes cajanderi to be the causative organism in a reddish brown, cubical rot of the heartwood of southern white cedar.

Both species are reported to have the same distribution, being found in coniferous and mixed forests of North America (Overholts, 1953; Lowe, 1957), Mexico (Guzman, 1973), Japan (Imazeki and Tsuguo, 1965), Britain (Rea, 1922), Scandinavia (Eriksson, 1958), and the European U.S.S.R. and Caucasia (Bondartsev, 1953).

The basidiocarp of Fomes roseus is sessile and typically ungulate in shape, with the pileus surface more or less incrusted. The context is pink or rose to vinaceous in colour. The tubes show varying degrees of stratification and a rose coloured hue similar to the context. The basidiocarp of Fomes cajanderi is typically applanate and otherwise of much the same colour and general appearance as Fomes roseus. Similarities between these two taxa have been sufficient for grouping them in the genus Fomes Gill. under the specific epithet roseus (Murrill, 1903). Fomes cajanderi has been given varietal rank in the species Fomes roseus as Fomes roseus var. eleganteus (Bresadola, 1911, cited in Bondartsev, 1953). Others have treated each taxon as a specific entity and subsequently grouped in one genus: Fomes roseus and Fomes subroseus (Overholts, 1953); Fomes roseus and Fomes cajanderi (Lowe, 1957); Fomitopsis rosea and Fomitopsis subrosea (Bondartsev, 1953). They have also been given specific status and treated in separate genera: Fomitopsis rosea and Fomes cajanderi (Nobles, 1971); Fomes roseus and Trametes subrosea (Weir, 1923).

The purpose of this study was to examine Fomes roseus and Fomes cajanderi in order to assess the taxonomic significance of traditional characters and to find additional characters which would help clarify the taxonomic status of these species.

Three main approaches were used in this study. First, morphological data from field specimens which included both substratum and basidiocarp characters, was assessed. This information was then correlated with results from developmental studies which yielded a number of characters not directly associated with gross appearance, such as the presence and distribution of different hyphal types. The importance of developmental studies to the taxonomy of the Polyporaceae was first realized by Corner (1932a). This approach, involving a microscopic analysis of hyphal types and their organization during the development of the basidiocarp, has been applied to Fomes cajanderi (Wong, 1973) but not to Fomes roseus. Analyses of hyphal development of both species were done in this study so that a reliable comparison could be made.

The second approach to this problem was to study the growth and development of isolates of Fomes roseus and Fomes cajanderi in agar and wood culture. Nobles (1971) has reviewed the taxonomic status of such data for many wood-rotting fungi. Features of agar cultures, such as the form and character of the advancing zone, colour, topography and texture of the mat, the presence or absence of fruiting areas, colour changes in the agar induced by the growth of the fungus, and hyphal characters are used by Nobles in her key to identifying cultures of wood-inhabiting hymenomycetes. Cultural characters of Fomes roseus and Fomes cajanderi led Nobles to believe

that distinct differences exist between these species in culture.

Experimental cultural studies such as the effect of temperature on growth rate and mating reactions have been carried out for Fomes roseus and Fomes cajanderi. Snell et al (1928) determined that Fomes roseus and Fomes cajanderi are distinct species based on growth rates in culture.

Mounce and Macrae (1937) have paired monosporous mycelia from both taxa distinguished on the basis of spore size. Because dikaryons were established among but not between isolates of each species, Mounce and Macrae have assumed that these taxa are sufficiently distinct to be maintained as individual species. Their results are supported by the work of Neuhauser and Gilbertson (1971). Pairing reactions were not undertaken in the study presented here.

Chemosystematic studies using thin layer chromatography as the separation technique were attempted. Chemical compounds were isolated from field collections and isolates in culture of Fomes roseus and Fomes cajanderi. In addition, collections of four other taxa were studied. Three of these are the type species of genera into which Fomes roseus and Fomes cajanderi have been placed. These additional genera were included not only to determine whether or not generic affinities could by chemically examined, but also to assess the significance of compounds peculiar to Fomes roseus and Fomes cajanderi.

To date, a number of authors have reported varying amounts of success in resolving taxonomic problems in basidiomycetes uning chromatographic techniques (Fries, 1958; Bonnet, 1959; Watson, 1966; Ito et al, 1968; Thoen, 1970; Thoen, 1975). Unfortunately, all of

the studies of this nature are qualitative comparisons of unidentified spots on chromatograms and only recently have attempts been made to identify specific fungal compounds, producing taxonomically useful chemical profiles (Arpin et al, 1974; Kirk et al, 1975; Yokoyama et al, 1975; Valadon, 1976; Favre-Bonvin et al, 1977; Arpin and Favre-Bonvin, in press). Even so, valuable information regarding taxonomic problems can be obtained by comparing a number of chemical characteristics of unidentified compounds isolated by chromatographic means.

The results of this study are presented in three sections. First is a detailed account of the development of Fomes roseus and Fomes cajanderi in nature. In the second, descriptions of the growth and development of these taxa in agar and wood cultures are presented. In the last section, results from a chemosystematic study are presented. The results and observations of these three sections are discussed with reference to the taxonomy of Fomes roseus and Fomes cajanderi.

MATERIALS AND METHODS

I. Field specimens

1. Gross morphology

Basidiocarps of *Fomes roseus* and *Fomes cajanderi* were obtained from the following herbaria: The Mycological Herbarium, University of Alberta (ALTA); The Herbarium, Northern Forestry Research Center, Canadian Forestry Service, Edmonton (CFB); The Cryptogamic Herbarium, University of Toronto (TRTC); and The National Mycological Herbarium, Biosystematic Research Institute, Ottawa (DAOM). In addition, research collections were made during the summer and fall of 1976 and 1977 (RC). A complete list of specimens examined is presented in Appendix I. Collections of *Fomes roseus* and *Fomes cajanderi* examined from various substrates are presented in Appendix II.

Dimensions of healthy basidiocarps representing as many developmental stages as possible, were taken on three axes: depth, or maximum distance between the margin and the substratum; thickness, or width halfway between the origin of the basidiocarp and the margin; diameter, or horizontal span of the basidiocarp on the substratum.

2. Hyphal analysis of basidiocarps

Hyphal analyses were carried out on specimens from the Mycological Herbarium, University of Alberta and from the research collections. Dried basidiocarps were soaked several minutes with, and mounted in, 10% aqueous KOH. Material taken from fresh basidiocarps within 48 hours of collecting, and from frozen specimens which had been allowed to thaw for 24 hours, was mounted in tap water. All preparations were examined

unstained and stained with 1% aqueous phloxine.

Hyphal organization of the basidiocarp was studied using three procedures. First, freehand sections made perpendicular to the pileus surface along transects drawn from the substratum to the margin were examined. Second, a small protion of the section was macerated by teasing apart the component hyphae. Line drawings were made with a camera lucida. Third, a macerated basidiocarp section was washed into a vial containing several mls of 1% aqueous phloxine. Several drops of the macerate were mounted. The third step, always used in conjunction with the first two, permitted a more detailed study of hyphae bearing chlamydospores.

The following zones of the basidiocarp were studied: margin, pileus surface, dissepiments, and context. The margin, a region of actively growing hyaline hyphae, constitutes the extreme distal zone of the basidiocarp, forming a light pink, to rose coloured band 500-2000μ in width. It is bound on the lower side by the first indications of dissepiment formation, and on the upper side by the pileus surface. The latter forms a layer of hyphae 400-1000μ thick over the upper surface of the basidiocarp, and is generally more deeply pigmented than are other zones. Sections of the pileus surface were rinsed with a 5.25% solution of sodium hypochlorite and washed several times with tap water before study. The dissepiments occur on the pileus undersurface and form a network of tissue, the porefield. Bounded on one side by the substratum and on all others by the zones mentioned, is the context.

Basidiospores were obtained from the following collections: Fomes roseus- RC 104, RC 106, RC 161, RC 163, RC 170; and Fomes

cajanderi- RC 3, RC 14, RC 105, RC 162, RC 195. Fresh collections were placed, pore surface down, on glass slides beneath an inverted beaker. Basidiospores were mounted in water and their lengths and widths measured immediately. Averages were used in a Chi square test to determine whether a significant difference in spore size exists between the two species.

3. Vegetative mycelium in natural substrata

Wood collected with and adhering to the basidiocarps in the research collections was presumed infected with the hyphae of the taxon represented by the attached basidiocarp. The development of the mycelium in the wood was studied using two methods. First, radial and tangential hand sections of the wood were mounted unstained in water. Second, slivers of the wood were macerated using the following prodedure. Several pieces of infected xylem approximately 5 mm in diameter and 1.0 cm in length were placed in vials containing one part superoxal (a 30% solution of H_2O_2) to four parts distilled water to five parts glacial acetic acid. The vials were then corked tightly and placed in an oven at 55-60^{o}C for 72 hours. Afterwards, the macerated xylem was washed three times with distilled water and preserved in 95% ethyl alcohol (after Purvis et al, 1966). Small amounts of the macerate were examined with phase contrast and bright field microscopy.

II. Isolates in culture

1. Preparation of isolates

Isolates not obtained as stock cultures on agar slants from

DAOM or ALTA were derived from the context and wood of field specimens. Portions of the context of living basidiocarps were excised using sterilized forceps, placed on 2% malt agar (Nobles, 1965), and incubated at room temperature in the dark for 7 or 8 days. Subcultures taken from the advancing marginal hyphae surrounding the tissue plug were incubated for one week under ambient room temperature and lighting before being used to inoculate slants and plates of 2% malt agar. The former were incubated at 3-5^{o}C as stock cultures while the latter were maintained in the laboratory for as long as five months by subculturing on 2% malt agar at two week intervals. Slivers of wood removed from the substratum directly beneath the basidiocarp were used in the same manner to initiate cultures.

Cultures on 2% malt agar started with inoculum from stock cultures were incubated for two weeks under the light and temperature conditions of the laboratory. Inoculum from the margins of these cultures was used to establish cultures for study.

2. Agar cultures

The following isolates were selected for cultural studies because they had previously demonstrated good growth and a propensity to form basidiocarps: Fomes roseus- RC 104, RC 106, ALTA B58, ALTA B182, DAOM 17572; and Fomes cajanderi- RC 105, RC 107, ALTA B19, ALTA B74, ALTA B119. Three plates of each isolate were incubated under the conditions of ambient light, temperature, and humidity. Culture characteristics were observed every 3 or 4 days for 5 weeks.

For hyphal analyses, sections of the mycelial mat of these

same cultures were mounted in distilled water, teased apart, and stained with 1% aqueous phloxine.

The presence or absence of extracellular oxidase was determined for two week old cultures using the gum guaicum test of Nobles (1958a).

A Chi square test of significant difference in spore size was done on spores collected by inverting plates with pore fields over glass slides.

3. Wood cultures

Slices of air dried xylem 3-7 mm thick and 30-40 mm long, from Picea, Pinus, Betula, Populus, Amelanchier, and Salix were soaked in distilled water over night. One slice of each genus was placed in a screw cap vial with 5.0 ml of distilled water and autoclaved for 20 minutes at 15 pounds psi. Two slices of each genus were inoculated with agar inoculum plugs 3.0 mm in diameter and incubated as were agar cultures. Examinations of the wood cultures were made weekly for four months.

The mycelium of isolates using Picea as substratum were analyzed three months after inoculation. The vegetative mycelium in the wood was studied using the same procedures as outlined for field specimens. The mycelium on the surface of the slices was removed and studied in the same manner as mycelium on agar.

4. Effect of temperature on growth rate of vegetative mycelium

Growth rates for eight isolates of Fomes roseus and nine isolates of Fomes cajanderi were calculated by measuring with callipers, the radial increase of cultures on plates of 2% malt agar. Inoculum

plugs were placed at the edge of plates and incubated in polyethylene bags in the dark at 22°C, 25°C, 28°C, 33°C, and 37°C. Readings were taken by holding the plate toward a light source provided by a 60 watt bulb. Two measurements were made per plate. Rate of growth was calculated on the basis of readings taken every 2 days for 16 days. For each isolate, four replicate plates were used. As this procedure was repeated once, the final figures are the averages of 10 to 16 measurements per isolate per temperature. Averages were used in a Chi square test to determine whether a significant difference in growth rate exists between the two species.

III. Chemosystematic studies using thin layer chromatography

In addition to Fomes roseus and Fomes cajanderi, the type species of genera into which the two taxa have at times been placed were included: Fomes fomentarius (L. ex Fries) Kickx, the type species of Fomes Gill.; Fomes pinicola (Swartz ex Fries) Cooke, the type species of Fomitopsis Karst.; and Trametes suaveolens (L. ex Fries) Fries, the type species of the genus Trametes Fries (Bond. et Sing. emend.). Fomes pini (Thore ex Fries) Karst., a representative species within the genus Phellinus Quel., in which the two taxa have never been place, was included for comparative purposes.

Vouchers for collections used for extraction are identified as follows: Fomes roseus- RC 104, RC 106, RC 159, RC 160, ALTA 2513, ALTA 7112; Fomes cajanderi- RC 128, RC 161, RC 162, RC 195, ALTA 6247, ALTA 6261; Fomes fomentarius- RC 213, RC 230; Trametes suaveolens- RC 210; Fomes pinicola- RC 214; and Fomes pini- RC 121.

Isolates of Fomes roseus and Fomes cajanderi were incubated on 2% malt agar for two months at room temperature and in the light of a south facing window. Those with rose coloured basidiocarps at the end of this period were used and are identified as follows: Fomes roseus- RC 106, DAOM 17572; and Fomes cajanderi- RC 107, ALTA B19, DAOM 73183.

For the preparation of crude natural extracts, the context of air dried basidiocarps was ground in a Kurzzeitbetrieb mill. Dried mats of cultured mycelium were used intact for extraction purposes.

The effectiveness of a number of solvents in extracting compounds with ring structures was examined. Ethyl acetate, methyl alcohol, and ethyl ether gave the best results. This was determined by adding several ml of concentrated H_2SO_4 to the extraction fluids. A colour change signified the presence of ring structures in the solvent. Depth and rapidity of colour development were criteria used to determine the effectiveness of the extraction fluid. Ethyl acetate was chosen as the extraction solvent.

In a screw cap vial, 1.5 gm of ground context were added to 20 ml of ethyl acetate and allowed to stand for 24 hours. The supernatant was decanted, placed in a tightly capped vial, and stored in the dark at room temperature. Several ml of extraction fluid were combined with several drops of H_2SO_4 to make preliminary determinations of the relative amounts of ethyl acetate soluble compounds present.

For chromatography, plates 20 X 20 cm and strips 5 X 20 cm precoated with a 0.25 mm layer of silica gel without gypsum

were spotted with 25-30 ul of extract. It was determined, after testing spot resolution in a number of developing solvents, that two solvent systems were required to effectively separate the compounds. These are listed as solvent A (acetone: benzene, 1: 4), and solvent B (benzene: methanol: acetic acid, 45: 8: 4). Development in one direction was sufficient to separate the compounds.

Compounds were detected using ultraviolet light, which causes cyclic compounds to fluoresce, and two reagents, indicators I and II. Indicator I contained 1.0% vanillin in a 4: 1 mixture of concentrated H_2SO_4: ethanol. It was prepared immediately before use and applied to developed chromatograms using a chromatography spray gun (Brinkman Instruments). Chromatograms were gradually heated to increase colour development. A purple colour indicated the presence of a double ring compound. Indicator II was prepared by combining in a one to one ratio, stock solutions of 3% aqueous $FeCl_3$ and 3% aqueous $K_3Fe(CN)_6$ after diluting each ten times with water. Plates were placed in a bath of this liquid, washed with a dilute solution of HCl, and air dried. A blue to violet colour indicated the presence of phenol moities. Spot patterns were recorded on a Xerox copying machine.

For isolating and purifying compounds for ultraviolet spectrophotometric analysis, TLC plates bearing streaks of extract were developed with a reference strip bearing a spot of the same extract. Compounds were located by applying the indicator to the developed reference strip. Compounds fluorescent with ultraviolet light could be detected directly. A reference strip was used with

every development as Rfs varied from day to day.

The location of a compound was outlined with a dissecting needle, scraped from the glass with a razor blade, and eluted with spectrograde methanol. The elution was evaporated until just enough remained to streak a TLC plate and spot a reference strip. These were developed and detection and elution procedures repeated. The compound was examined with a Unicam SP 1800 ultraviolet spectrophotometer. Results were recorded on a Unicam AR 25 linear recorder (see Appendix IV). Purified compounds were hydrolyzed by heating with 10 ml of 2N HCl in a reflux column. The hydrolysate was evaporated to dryness and separated in ether and water. The water fraction was discarded while the ether fraction was evoporated to dryness, dissolved in spectrograde methanol, and scanned with the ultraviolet spectrophotometer.

RESULTS

I. Field specimens

1. Basidiocarp morphology

Fomes roseus and *Fomes cajanderi* exhibit similar variations in basidiocarp morphology. These variations are described separately for each taxon. Descriptive terms are from Overholts (1953).

Basidiocarps of *Fomes roseus* range from: 1.5-10.0 cm in diameter; 0.9-7.0 cm in height; and 1.3-3.0 cm in depth (Figure 1). They are rarely resupinate, usually sessile and may be effused-reflexed, convex to ungulate, and either solitary or in groups on the substratum. Occasionally, two or three basidiocarps in close proximity are laterally fused to a small degree. Imbricate forms are uncommon. Pilei are generally dimidiate.

Basidiocarps of *Fomes cajanderi* (Figure 2) range from: 0.7-20.0 cm in diameter; 0.4-1.4 cm in height; and 1.0-4.0 cm in depth. They are rarely resupinate and usually effused-reflexed. They are applanate to conchate or convex, occasionally ungulate and rarely solitary. Quite often, particularly on fallen tree stems where numerous basidiocarps have formed in close proximity, the lateral margins of neighbouring basidiocarps are fused to form an oblong band in which the identity of individuals is not always discernible. Frequently, basidiocarps are imbricate, with bases fused to form a confluent mass. Single pilei are dimidiate to subreniform.

Basidiocarps of *Fomes roseus* are woody to corky, and never

coriaceous as are the basidiocarps of Fomes cajanderi. Basidiocarps of the latter species are often corky.

The pileus surface of Fomes roseus varies from cream, pale pink, tan, brown or grayish brown, to charcoal black. The latter colour occurs in young and old specimens. The pileus surface is minutely tomentose to glabrous, rarely smooth and usually slightly rippled to hummocky. A thick superficial layer of soft matted hyphae, usually found in young specimens, and occasionally present in the vicinity of the margin of older specimens, gives a rubbery texture to the pileus surface. Older specimens are often incrusted and rimose.

In Fomes cajanderi, the pileus surface can be cream, or grayish, pale pink, rusty or vinaceous brown, to charcoal black. The latter colour occurs in young and old specimens. The pileus surface is glabrous to minutely tomentose, and either smooth or hummocky. Occasionally, numerous small tubercles are present. A layer of thick, soft, matted hyphae on the surface of young specimens and adjacent the margin of older basidiocarps, creates a fibrous or occasionally rubbery texture. Older specimens are sometimes incrusted and rimose.

Concentric striations on the pileus surface of some basidiocarps of Fomes roseus are the result of slight gradations in colour and/or shallow grooves. Occasionally, striations are absent or obscured by thick deposits of a brown to black amorphous substance.

Concentric striations are more frequent in Fomes cajanderi where they are gray to brown in colour and often accentuated by shallow grooves or ridges. Only rarely are they obscured by deposits of dark, pigmented material.

The margin of Fomes roseus is an obtuse band of cream or rose coloured sterile tissue. Black, incrusted margins are frequent in very old specimens and basidiocarps growing on exhausted substrata.

In Fomes cajanderi, the margin in young specimens is a thick, obtuse band of sterile, pink to vinaceous tissue. In older specimens, the margin becomes acute, or rarely, remains obtuse. The margins of old or senescing individuals are brown or occasionally black.

In Fomes roseus, the cream to pink to vinaceous brown context is thick and fibrous. In a median longitudinal section, light to dark brown growth lines of varying intensity, running concentric to the boundary of the margin, are always present. The context is brown to black when spotted with 10% KOH.

The context of Fomes cajanderi is pink to vinaceous brown and corky to fibrous. The growth lines observed in Fomes roseus are apparently identical to those of Fomes cajanderi. The context is black when treated with KOH.

The pore surface of Fomes roseus is smooth or gently undulating, and cream to pink to vinaceous brown in colour. It is horizontal or sloped slightly to sharply from the margin to the substratum and has round to slightly angular pores, 2-6 per mm.

The pore surface of Fomes cajanderi is smooth or gently undulating, and cream to pink to vinaceous brown. Since the great majority of specimens are effused-reflexed, the pore surfaces are horizontal below the pileus, sloping gradually to sharply toward the substratum. Tubes developing on the effused portion of the basidiocarp have angular, vertically elongated, daedeloid pores.

Pores average 2-6 per mm.

Tube layers are stratified in both taxa. A whitish hyphal growth filling the tubes of the older strata, and the continuum formed by the dissepiments of each tube layer with the next, may obscure the identity of individual tube layers.

2. Substratum

Fomes roseus and Fomes cajanderi most often were found growing on the dead wood of standing or fallen species of Picea. Other genera providing substrata were Pinus, Larix, and Populus. Specimens of Fomes cajanderi on Abies, Pseudotsuga, and Prunus were also examined. Numerous collections of both species from unidentified coniferous wood were studied. There is no apparent correlation between basidiocarp morphology and the identity of the substratum. A list of collections examined from various substrata is presented in Appendix II.

Wood infected with either species displays a dry, brown cubical rot of the sapwood and heartwood. In less decayed wood, zone lines may be observed as narrow or broad, wavy, reddish brown lines in the wood.

3. Hyphal analysis

The development and microstructure of basidiocarps of Fomes roseus and Fomes cajanderi were found to be very similar. For this reason, there follows a microstructural description of the development of Fomes roseus from the vegetative phase in the substratum, to the mature sporulating basidiocarp. Fomes roseus and Fomes cajanderi are compared with respect to their development

following the developmental analysis of Fomes roseus.

Terminology applying to the types of hyphae in the basidiocarp is taken from Corner (1953). He described skeletal hyphae as "...unbranched, thick-walled, commonly aseptate...hyphae"; and generative hyphae as "...thin-walled, branching, septate hyphae."

A. Basidiocarp development in Fomes roseus

a. Mycelium in wood

The mycelium is largely confined to the lumina of the tracheids (Plate 1a) where thick-walled hyphae, 1.9-6.0μ in diameter, and thin-walled, clamped hyphae, 1.3-3.4μ in diameter, are present in varying amounts. The thick-walled hyphae are hyaline to brownish, and grow through the tracheid lumen parallel to the long axis of the wood cell, until adjacent to a ray. At this point, numerous lateral hyphal branches, 1.1-4.2μ in diameter, form at right angles to the thick-walled parent hyphae to create a dense mass of intertwining hyphae. The thin-walled hyphae also grow through the tracheid lumen parallel to the long axis of the wood cell. These hyphae also grow laterally from cell to cell through bordered pits or bore holes.

Masses of thick-walled, brownish hyphae and deposits of a reddish brown amorphous substance are present in the tracheids of the zone lines.

b. Primordia

Emerging through cracks in the wood or bark from areas where particularly heavy hyphal aggregations occur, are clamped generative hyphae, 1.2-2.8μ in diameter, and infrequently branched skeletal

hyphae, 1.0-3.4μ in diameter. These grow together in a radial pattern to form a compact knob of dense mycelium, the first indication of primordium formation. Primordia are incipient basidiocarps which lack pore development. They grow closely appressed to the surface of the substratum, forming velvety, cream to pink or vinaceous, pulvinate pads, 2.0-7.0 mm in diameter (Figure 3).

Skeletal hyphae are hyaline to faint vinaceous brown, occasionally having one to several constrictions along their length. Generative hyphae are clamped, hyaline, and deeply staining. The velvety surface of the primordium is due to the rounded or slightly tapered apices of skeletal and generative hyphae protruding from the main mass of hyphae.

Dark, reddish brown pigment deposits in, and on the skeletal hyphae produce brown patches on the upper surface of some primordia. The primordium becomes a sporulating basidiocarp following the development of pores on the undersurface. Further differentiation yields the mature basidiocarp.

c. Mature basidiocarps

i. Margin

The margin (Figure 4a) consists of loosely woven skeletal and generative hyphae growing parallel to the direction of basidiocarp growth. Skeletal hyphae are smooth, relatively thin-walled, rarely branched, hyaline to pale reddish brown, and 2.5-6.0μ in diameter. The tips of the skeletal hyphae, some of which protrude several microns from the margin, are smooth and rounded, or slightly tapered, or swollen (Figure 5a). The cytoplasm of the tip is granular and stains deeply. Behind the tip, the contents of the

lumen stain faintly or not at all. The lumen is very regular and uniform in young skeletal hyphae, becoming slightly irregular in older ones. In some basidiocarps, up to five septa occur in the thin-walled terminal regions of the skeletal hyphae (Figure 5b). These septa form at regular intervals of approximately 15-20μ. Walls of the skeletal hyphae occasionally have hyaline, asymmetric, phlange-like projections, 1.0-4.0μ in length (Figure 5c). Young skeletal hyphae form either from the tips of older skeletal hyphae, or from terminal cells of generative hyphae. In the first case, the terminal 12.0-15.0μ of a skeletal hypha becomes swollen and fusiform. The thin wall of the tip protrudes, elongates, and widens, leaving a constriction 2.0-4.0μ in diameter, dividing old and new portions (Figure 5d).

Skeletal hyphae which originate from generative hyphae are subtended by clamp connexions (Figure 5e). As the young skeletal hypha elongates, its diameter increases from 2.0-3.5μ next to the clamp, to 2.5-6.0μ at its widest point.

Skeletal hyphae perpendicular to the direction of basidiocarp growth, occur 100-500μ from the edge of the margin (Figure 6). These have irregular lumina, frequent areas of thickening in the walls, and numerous phlange-like projections. Occasionally, short solitary thick-walled branches, 10-30μ in length, occur at acute angles to the main axes of these hyphae. Lateral branches, 3 to 4 in number, grow from the apices of skeletal hyphae in some basidiocarps (Figure 7).

Generative hyphae are not as prevalent as skeletal hyphae. They are arranged parallel to the direction of growth, are

1.5-3.5μ in diameter, and stain deeply. Clamp connexions are frequent and serve as points of origin for lateral branches which arise from, or immediately adjacent to them (Figure 5f). Branches soon orient themselves parallel to the direction of growth. Generative hyphae are usually evenly dispersed among the skeletal hyphae, but are occasionally found in small, dense clusters.

In some basidiocarps, approximately 200-400μ from the margin edge, thin-walled, globose to fusiform chlamydospores, 5.0-18.0μ in diameter, occur. They are formed in linear series on thin-walled hyphae, 1.5-3.0μ in diameter (Figure 8, Plate 2a,b).

ii. Pileus surface

The pileus surface (Figure 4b) represents a developmental continuum from the youngest area immediately adjacent to the margin, to the oldest, bordering on the substratum (Figures 9 and 10).

Hyphae of the upper surface are negatively geotropic, and grow perpendicularly to the direction of basidiocarp growth. Near the margin, the skeletal hyphae have moderately thick, hyaline to slightly pigmented walls. The distal 200-300μ sections of skeletal hyphae form a palisade with little or none of the amorphous pigmented materials present. Generative hyphae vary in their staining response to phloxine. Occasionally, these hyphae are thick-walled and irregular. Particularly heavy deposits of wall material occur around easily fractured clamp connexions (Figure 11).

In older areas of the pileus surface, thick-walled tips of skeletal hyphae, forming the palisade, become broken or sharply truncated (Figure 9). An amorphous, reddish brown, agglutinating substance becomes very prominent between the hyphae of older regions

(Figure 10). Embedded in this substance, which may build up beyond the tips of the hyphae, are numerous foreign particles such as xylary elements, pollen grains, and fungal spores. Walls of the skeletal hyphae are hyaline to reddish brown, and the lumen is almost, or entirely occluded. Generative hyphae are rarely irregular, thick-walled, and knobby. These form in scattered fragments or dense masses.

iii. Context

The context (Figure 4c) is composed primarily of skeletal hyphae of two types: smooth hyaline to faint reddish brown hyphae, 2.5-5.0μ in diameter, oriented parallel to the direction of basidiocarp growth; and irregular, occasionlly branched hyphae, 3.2-6.0μ in diameter, perpendicular to the former. Both types of skeletal hyphae have thin, occluded lumina and phlange-like projections (Plate 1b).

The irregular skeletal hyphae produce branches at right or acute angles to the main axis. These are constricted at the base, and remain slightly less in diameter than the parent hypha.

Dense masses of thin-walled, rarely clamped, deeply staining, incrusted hyphae, 2.0-3.5μ in diameter, occur scattered thoughout the context of some basidiocarps.

Generative hyphae as described in the margin, are not present in the older regions of the context, but may occasionally be found in areas of the context close to the margin. Clamped hyphae, when present in the older areas, are brittle and thick-walled, with narrow, sinuous lumina (Figure 11, Plate 3a). These are scattered in

groups among the skeletal hyphae. Chlamydospores similar to those of the margin, were scattered throughout the context of some basidiocarps.

Constrictions in the skeletal hyphae occur most frequently in the growth lines of the context. Large amounts of the agglutinating substance surround the hyphae of the growth lines.

iv. Dissepiments (Figure 4d)

Hyaline to faint reddish brown skeletal hyphae, 2.0-4.0μ in diameter, and abundantly clamped generative hyphae, 2.0-4.0μ in diameter, are the hyphal types of this area. The former have few constrictions, and are contorted, knobby, branched, and tightly woven (Figure 12a).

Adjacent to the margin, generative and skeletal hyphae grow geotropically to form tufts of parallel hyphae, perpendicular to the plane of the undersurface. Skeletal hyphae originate from generative hyphae, and rarely have constrictions along their length.

Generative hyphae (Figure 12b) grow parallel to the skeletal hyphae, until turning abruptly toward the surface of the dissepiments to form basidia (Figure 12c). Basidia are clavate and cylindrical, 4.2-6.3μ X 13.0-17.0μ, and form a palisade lining the vertical surfaces of the dissepiments. They are each subtended by a clamp connexion, and produce spores at the apices of four hyaline sterigmata, approximately 4.0μ in length.

Basidia are not formed beyond a point 30μ from the growing edges of the dissepiments. In upper regions of tubes, masses of thin-walled generative hyphae form a white cottony plug-like mass of mycelium. The walls of the tubes adjacent to this mass lack

basidia.

Basidiospores are cylindrical and slightly curved above the region of the hilar apiculus, which forms lateral to the pole adjacent to the basidium (Figure 13a). Spore cytoplasm stains intensely, revealing one to four spherical refactive bodies within the cytoplasm. Basidiospore size ranges from 4.9-7.3μ X 2.6-3.2μ. An average of fifty basidiospores from five collections is 2.9 X 6.5μ.

B. Fomes cajanderi compared

a. Mycelium in the wood and primordium formation

In Fomes cajanderi, the vegetative mycelium in the wood and the pattern of primordium development do not exhibit any visible differences from Fomes roseus. Hyphal types, their proportions, and their development are apparently identical. Primordia lack distinguishing features at the microscopic and macroscopic levels.

b. Mature basidiocarp

i. Margin

There were no detectable microscopic differences in margin development between the two taxa. The thinner, more acute margin of Fomes cajanderi appears to be composed of generative and skeletal hyphae in equivalent proportions to those constituting the more obtuse margin of Fomes roseus.

ii. Pileus surface

The palisade forming the upper surface of basidiocarps of Fomes cajanderi tends to have lesser amounts of the amorphous interhyphal agglutinating substance than does Fomes roseus.

However, in both species this characteristic is difficult to evaluate, as the quantity of the substance not only varies among basidiocarps, but may also be present in a bleached condition. Otherwise, development of the pileus surface of the two species is identical.

iii. Context

Hyphal types and their proportions are the same in the context of both taxa. There is, however, a tendency for the walls of skeletal hyphae of Fomes cajanderi to be slightly darker than their counterparts in Fomes roseus.

iv. Dissepiments

The only equivocal difference in the dissepiments are the spores which, in Fomes cajanderi (Figure 13b), range from 4.5-7.5μ X 1.7-2.9μ. The average size of fifty spores from five collections was 7.3 X 2.6μ. A Chi square test does not show average spore sizes to be of significant difference between the two taxa.

II. Isolates in culture

Since only very slight differences were observed between the two species in culture, the macroscopic and microscopic featues of Fomes roseus are described. Distinctions exhibited by Fomes cajanderi are noted.

1. Gross features

a. Agar culture

Within two or three days following inoculation, fine, monopodially branched hyphae grow away from the inoculum plug in a radial pattern. These hyphae grow closely appressed to, or

slightly below the agar surface. Behind the advancing margin develops a zone of aerial hyphae which produces a cottony to flocculent growth, 0.5-3.5 mm thick. As the mycelial mat increases in diameter, the margin forms an uneven, whitish band, circumscribing the dense white to faint pink mycelium. The margin maintains a width of 2.0-4.0 mm until reaching the edge of the plate. Depending upon the isolate, coverage of an 8.5 cm plate requires 19 to 22 days for Fomes roseus. Fomes cajanderi requires 18 to 20 days. Below the mat, the agar remains opaque, or develops a brownish colouration, particularly in the vicinity of the inoculum plug.

A positive test for extracellular oxidase is the formation of a blue colour following the application of several drops of alcoholic gum guaicum to the culture mat. Positive reactions, when they occurred, were faint. For several isolates, tests of replicate culture plates did not yield consistent reactions.

Indications of basidiocarp development become apparent 20 to 30 days following inoculation. In some cultures, basidiocarps develop earlier, particularly when they develop on the upper surface of the inoculum plug. Basidiocarps usually develop adjacent to the margins of plates but occasionally they form scattered over the surface of the mat. They grow either appressed to the vertical surface of the plate or in a continuous to discontinuous circular band, 0.5-15.0 mm in width, and 0.5-4.0 mm from the plate edge. Thick pads of dense, felty mycelium having an accentuated pink or brownish colouration, are the first signs of basidiocarp initiation. Where primordia develop several millimeters interior to the

walls of the plate, the intervening area is composed of pale, cottony to flocculent mycelium similar to the central regions of the culture mat.

Pores form on the upper surface of the primordium within 2 to 5 days. Thick ridges of slight vertical development on the upper surface are the first indications of pore formation. Within 4 to 7 days, vertical development of these ridges occurs, and the intervening furrows become recognizable as pores. These range from 0.5 to 1.5 mm in depth, and may be daedeloid or poroid. Discharged basidiospores form a thick cream coloured deposit on the lids of inverted plates. When plates are not inverted, basidiospores are cast to the bottom of the tubes where they eventually form a reddish brown to almost black deposit.

b. Wood culture

Neither species demonstrated a preference for any one of the wood genera used as substrate. With in 2 to 3 weeks following inoculation, small amounts of white, cottony mycelium develop along the upper transectional surfaces of the wood slices. Within 2 weeks following, mycelium develops on the longitudinal surfaces. Fomes roseus usually develops scattered clumps of hyphae over the wood surface. Fomes cajanderi tends to produce a uniform layer of hyphae which covers the surface of the wood slice. Mycelium remains white to faint pink unless allowed to dry out, when it becomes tan to light brown in colour.

Knots of hyphae, 0.5-1.5μ in diameter, indicating incipient basidiocarps, appear 2 to 3 months after inoculation. One to 20

pink to vinaceous brown, hemispherical primordia form on each slice. Pore fields of daedeloid, angular or circular pores form on the upper surfaces of the primordia in the same manner as in agar culture. Occasionally, vertical corrugations develop on the lateral surfaces of the basidiocarp. This type of dissepiment configuration is the result of lateral elaboration of hyphae on well defined vertical zones, 0.5-1.0 mm in diameter. The result is fertile vertical grooves which resemble median longitudinal sections of elongated tubes.

The wood slice exhibits a faint brown, cubical rot within five months of inoculation.

2. Hyphal analysis

Terminology applying to hyphae observed in culture is from Nobles (1958b; 1965). Nodose-septate hyphae are thin- or thick-walled hyphae bearing clamp connexions. Fibre hyphae have thick, refractive, hyaline or brown walls, with a narrow or absent lumen. They lack clamp connexions and septa.

a. Agar culture

The margin of the mycelial mat is a zone of frequently branched, thin-walled, nodose-septate hyphae, which range in diameter from 1.5-5.0μ. Approximately 2 to 4 mm in from this zone, mycelium is composed of intertangled, nodose-septate hyphae and fibre hyphae, with the latter predominating. The nodose-septate hyphae are thin-walled, abundantly clamped, frequently branched, and 1.5-3.6μ in diameter. Fibre hyphae are present in a number of developmental stages. They originate immediately adjacent to clamp

connexions as elongated terminal cells (Figure 14). These aseptate cells elongate and increase in diameter as the densely staining hyphal tips grow away from the subtending clamps. Fibre hyphae range in diameter from 1.5 to 3.8μ in the region immediately adjacent to the clamp connexion; to 3.5-5.0μ in the central area, to 1.3-4.4μ in the apical regions. Some are branched in the apical region (Figure 15).

Irregular, thick-walled nodose-septate hyphae, 1.3-4.3μ in diameter, occur in isolated patches (Figure 16, Plate 3b). These hyphae have swollen clamp connexions and solid knob-shaped protuberances projecting from the walls.

Thin-walled, nodose-septate hyphae bearing numerous branches, grow beneath the surface of the agar and occasionally become irregular and thick-walled. Intercalary, fusiform to globose, thin-walled chlamydospores, 13-20μ X 5-20μ, occur on submerged and aerial mycelium. They are consistently solitary (Figure 17). The occurence of chlamydospores in culture is erratic and not correlated with particular isolates.

Primordia are composed of nodose-septate hyphae and fibre hyphae which develop and grow upward from the culture mat surface. Closely interwoven, these hyphal types appear to lack a particular arrangement within the primordium. Thin-walled, nodose-septate hyphae, which predominate in very young primordia, become less prevalent than fibre hyphae as the primordium increases in size. In large primordia, nodose-septate hyphae are found in localized masses. Often, they become irregular and thick-walled and have narrow sinuous lumina. Fibre hyphae are rarely branched.

The first indication of pore formation is the upward growth of fibre hyphae and nodose-septate hyphae. This produces a net-like pattern of ridges on the upper surface of the primordium. Pores up to 2.4 mm deep, form 4-6 per mm. Pore mouths range in shape from daedeloid to circular.

Lining the walls of the pores and forming from the clamped terminal cells of nodose-septate hyphae, is a well defined palisade layer of clavate basidia, 5.2-8.1 X 14.0-20.0μ in size. Up to four slender, hyaline sterigmata, 2.5-3.5μ in length, are present on the apices of mature basidia. The basidial palisade develops approximately 30-70μ behind the advancing zone of hyphae forming the pore walls.

Basidiospores are smooth, narrow, cylindrical, and slightly curved, particularly above the hilar apiculus. Spores of Fomes roseus are 5.1-7.0 X 2.6-3.1μ in size. An average size for fifty basidiospores from five isolates was 6.5 X 2.9μ. Basidiospores of Fomes cajanderi range from 4.0-8.0 X 1.7-2.7μ and average 7.4 X 2.6μ. A Chi square test did not show the spores of the two taxa to be significantly different in size.

b. Wood culture

In the wood, thin-walled, clamped hyphae, 1.5-3.5μ in diameter, grow in a sinuous manner through the lumina of the tracheids. Dense aggregations of closely intertwined, thin-walled hyphae occur in the vicinity of the ray cells. The thin-walled hyphae grow from cell to cell through bordered pits or bore holes. Medallion clamps are rarely formed. Thick-walled hyphae are hyaline and less prevalent than in naturally infected substrata. They occur growing

in a sinuous manner through tracheids.

Hyphae on the surface of the wood are of two types: nodose-septate hyphae, 1.0-4.0μ in diameter; and fibre hyphae, 1.3-4.0μ in diameter. These two hyphal types are closely interwoven. Single, intercalary, thin-walled chlamydospores, 8.0-15.0 X 5.0-12.0μ, occasionally form on nodose-septate hyphae. Clamp connexions often serve as points of origin for branches. Irregular, thick-walled, nodose-septate hyphae having swollen, solid clamp connexions and irregular refractive walls, are observed either in fragments or localized clusters. Infrequently branched fibre hyphae have thick, hyaline to faintly pigmented walls surrounding thin or occluded lumina.

Translucent, octahedral crystals are always present among the surface hyphae.

Primordia have randomly organized, closely interwoven nodose-septate hyphae and fibre hyphae. Deeply staining, branched, nodose-septate hyphae, 1.3-4.0μ in diameter, occur dispersed throughout the primordium and in localized masses. Irregular, thick-walled, nodose-septate hyphae form in scattered clusters.

Refractive to faintly pigmented, closely interwoven fibre hyphae, 1.7-5.0μ in diameter, constitute the major hyphal type of the basidiocarp. The velvety surface of the basidiocarp is due to the projection of numerous tips of fibre hyphae and, to a lesser extent, nodose-septate hyphae, beyond the main mass of the primordium.

Pores develop on the upper surfaces of the primordia. Pore walls, initiated as slight ridges, are composed of densely interwoven hyphae. Typical of these ridges are knobby, contorted fibre

hyphae. The upward growing edges of the dissepiments are composed of parallel, unbranched, thin-walled hyphae. Thin-walled, nodose-septate hyphae are less numerous and form in closely interwoven masses along the pore walls.

A uniform and sometimes discontinuous palisade of clavate basidia, 12.0-20.0 X 5.0-10.0μ in size, forms on the flanks of the dissepiments. Basidia are always subtended by clamp connexions. Basidiospores are identical to those formed in agar cultures.

3. Effect of temperature on growth rate of vegetative mycelium

The 17 isolates can be divided into three groups based on their optimum growth rate temperature. Fomes roseus isolates RC 106, ALTA B168, ALTA B182, DAOM 22629, DAOM F2381, and DAOM 17572 all had growth optima at 25°C. Fomes roseus isolates RC 104, ALTA B287, and Fomes cajanderi isolates ALTA B27, ALTA B189, DAOM 17529, DAOM 155908, DAOM 73183, and DAOM 17522 exhibited optimum growth at 28°C. The three remaining isolates of Fomes cajanderi, ALTA B19, ALTA B74, and RC 107, had growth optima at 33°C. Most isolates did not produce detectable growth at 37°C. Isolate Fomes roseus DAOM 17572 ceased to grow at 33°C. Results are displayed graphically in Figure 18. Curves of average growth rate of the two species are not statistically different at the 0.05% level of significance.

III. Chemosystematic studies using thin layer chromatography

Ethyl acetate was the most effective solvent in solubilizing cyclic compounds from ground mycelium. These compounds were also

soluble in petroleum ether, ethyl ether, and methanol. Water, hexanes, and ethyl alcohol did not solubilize detectable amounts of cyclic compounds.

Of the six taxa: Fomes roseus, Fomes cajanderi, Fomes fomentarius, Trametes suaveolens, Fomes pinicola, and Fomes pini, only Trametes suaveolens failed to yield substantial amounts of ethyl acetate soluble cyclic compounds. The five remaining species yielded ethyl acetate soluble compounds which reacted with concentrated H_2SO_4 to give yellow and brown colourations to the extraction fluids. Information derived from developing the extraction fluids by thin layer chromatography, with corresponding spectral data, is summarized in Table 1. Chemical profiles obtained from different samples of the same species, in cases where more than one sample was used, were very similar, if not identical. Distribution among the six species of the five compounds characterized is summarized in Table 2. A representative thin layer chromatogram is illustrated in Appendix III.

Phenols I and II failed to separate well in solvent A, but were detectable by their colour reactions with indicator I. With this indicator, phenol I was violet and phenol II was indigo. Solvent B separated phenols I and II very well. Benzotropolones I, II, and III separated well in solvent A, but were poorly resolved in solvent B.

Strong fluorescence with ultraviolet light was exhibited by phenols I and II. Benzotropolone III fluoresced weakly. Benzotropolone I and phenols I and II gave positive reactions with indicator

II, which indicates the presence of phenol moities. Indicator II did not react with benzotropolones I and II.

Acid hydrolysis and spectral analysis did not reveal the presence of sugar moities on any of the compounds. All of the compounds described here were present in Fomes roseus and Fomes cajanderi. Additional compounds occurring in the developed chromatograms of the other four species were not considered.

Benzotropolones I, II, and III had the widest distribution, being present in all but Trametes suaveolens which contained only a trace of benzotropolone I. None of the remaining four compounds was detected in this species. Phenol II was present only in Fomes roseus and Fomes cajanderi. Fomes pini contained a trace of phenol I which was otherwise present only in Fomes roseus and Fomes cajanderi.

Compounds produced in isolates of Fomes roseus and Fomes cajanderi in agar culture had TLC profiles which were virtually identical to those obtained from extracts of natural basidiocarps.

DISCUSSION

I. Field specimens

Gross features of field specimens were found to be directly dependent upon underlying hyphal characteristics. For this reason, results from studies of gross morphology, hyphal structure, and development of the basidiocarp of both species are discussed together with reference to previously published work.

Substrate characteristics do not provide distinctive characters for the separation of Fomes roseus and Fomes cajanderi. Weir (1923) states that Fomes roseus is confined to coniferous wood, while Fomes cajanderi may be found on coniferous and angiospermous wood. This is not an acceptable distinction, as Fomes roseus is also found on angiospermous wood.

Weir (1923) also states that the decay produced by Fomes cajanderi is "usually of a darker colour" than that produced by Fomes roseus. My observations do not substantiate this statement. Both species produce a dry, brown, cubical rot of the heartwood and sapwood. Rot characteristics in naturally infected wood are difficult to assess accurately on comparative terms. Variables, such as duration of decay, environmental influences, and the degree of interaction of other organisms, cannot be adequately evaluated.

Environmental preferences of the two species, particularly with respect to moisture,are probably not as distinct as Snell et al (1928) imply. They state that Fomes roseus is better adapted for

living and fruiting on dry, hewn timbers than is Fomes cajanderi, which prefers moist shaded environments. My observations do not substantiate this conclusion. I have examined two collections, each from a different locality, which contained typical basidiocarps of both species, and which had been growing on the same log, under the same environmental conditions. I have also examined basidiocarps of Fomes roseus from low-lying shaded areas and once collected basidiocarps of Fomes cajanderi on an exposed railroad tie.

Studies of hyphal configurations of both species in natural substrata did not reveal taxonomically useful information. In both species, thick-walled, brownish hyphae are quite noticeable in the tracheids of decaying wood. Thin-walled, clamped hyphae are also present growing laterally from cell to cell through bordered pits and bore holes. Wong (1973) reports the presence of thin-walled, clamped, hyaline hyphae in wood infected with Fomes cajanderi. He also makes reference to thick-walled, brown, aseptate, occasionally branched hyphae, 0.9-3.5μ in diameter, completely filling the tracheids in the advanced stages of decay.

Basidiocarp primordia are uniform in anatomy and morphology between these species and are not useful as a source of taxonomic criteria.

The major source of criteria for distinguishing between Fomes roseus and Fomes cajanderi is the mature basidiocarp. For both species, variation in basidiocarp shape, from applanate to ungulate, is generally acknowledged, although Rea (1922) neglected to include, or was not aware of this variation. He describes the

basidiocarp of Fomes roseus as being "hoof shaped" and that of Fomes cajanderi (Fomes carneus Nees) as being "thin". Bondartsev (1953) also recognized only the ungulate condition in the basidiocarp of Fomes roseus (Fomitopsis rosea (Alb. et Schw. ex Fr.) Karst.) and reported those of Fomes cajanderi (Fomitopsis subrosea (Weir) Bond. et Sing.) as being thin, flat, and never ungulate. He considered shape differences to be of prime importance in distinguishing these taxa. I maintain that this distinction is not at all reliable. Wong (1973) observed the formation of ungulate basidiocarps, particularly in young specimens, in Fomes cajanderi. Basidiocarp shape in these species, as in most members of the Polyporaceae, is extremely plastic. The pattern of the tubular hymenophore depends to a great extent on the location of basidiocarp formation on the substratum and other environmental influences. Size and shape differences of the basidiocarp are not correlated with the presence or absence of different hyphal types or their proportions.

Features of the pileus surface have often been given great emphasis in the taxonomy of polypores (Pegler, 1973). In spite of great variations in its appearance, I found the pileus surface of Fomes roseus and Fomes cajanderi to have a common and fundamental hyphal anatomy. This consisted of entire, broken, or truncated skeletal hyphae forming a palisade configuration. Between the hyphae of the palisade are large amounts of an amorphous, agglutinating substance which may be dark reddish brown, or colourless, if bleached. Bondartsev (1953) observed the hyphae of the pileus surface of Fomes roseus to be branched. I did not observe branched hyphae in the crust of any of the speicmens I examined. Variations

in gross features depend a great deal on extrahyphal features such as the amount and condition of the reddish brown agglutinating substance. Both taxa exhibit similar ranges in colouration of the pileus surface. Deep pigmentation is indicative of large deposits of the amorphous, reddish brown pigment. As these deposits thicken and build up between, and beyond the tips of the hyphae which form the palisade, a crustose layer is formed on the basidiocarp surface. Both taxa can be incrusted, although it is frequently more obvious in Fomes roseus. Overholts (1953) and Wong (1973) insist that the pileus surface of Fomes cajanderi is not incrusted at any stage. This does not agree with my observations.

Zonation of the pileus surface is not a consistent feature in either species. I found it to be generally more pronounced in Fomes cajanderi than in Fomes roseus. Overholts (1953) considers the pileus surface of Fomes roseus "usually azonate", while Bondartsev (1953) notes that it is "somewhat concentrically striated". Weir (1923) does not consider zonation a feature of the "normal" pileus surface of this taxon. According to Weir (1923), Fomes cajanderi (Trametes subrosea nom. nov.) has a "conspicuously narrow zonate" surface, the zonation of which is "often obscured by a revival of growth". Overholts (1953) considers the pileus surface of Fomes cajanderi "often zonate", while Peck (in Neuman, 1914), Bondartsev (1953), Lowe (1952), and Wong (1973) describe it simply as "zonate or azonate".

Austwick (1968), in his consideration of the factors influencing "zonation of fruit body tissue", defines zones as

"regions differing in colour and texture which represent the positions of the margin at different times during the growth of the fruit body, thus reflecting the suitability of the environmental conditions for growth". He states that zone formation is the result of the "slowing up" of hyphal elongation, thus causing protoplasm and pigment accumulation in hyphal tips. Zonation then, should occur in both species if indeed Austwick's theory is correct. Zonation is easily obscured, not only by revival of growth as noted by Weir (1923) in Fomes cajanderi, but also by the patchy to even deposition of the amorphous pigmented material so characteristic of the pileus surface of both species.

From my observations and those of Lowe (1957), the margin of vigorous specimens of Fomes roseus is an obtuse band of sterile tissue. Others have observed it to be acute or rounded (Overholts, 1953), or sharp, becoming blunt (Bondartsev, 1953). In Fomes cajanderi the margin is usually obtuse in young specimens, becoming acute with age. Overholts (1953) considers the acute margin to be only usually the case. My observations support those of Overholts, as margin thickness is not consistent in Fomes cajanderi, although there is a definite tendency for the margin of this speices to be thinner than that of Fomes roseus. The thinner, more acute margin of Fomes cajanderi is composed of generative and skeletal hyphae in equivalent proportions to those constituting the more obtuse margin of Fomes roseus.

Skeletal hyphae develop in the margin from the clamped apical cells of generative hyphae. There is some controversy over the application of the name "skeletal hyphae" to these thick-walled

terminal structures. Traquair (1974) suggested they be called "skeletal cells", whereas Smith (1966) and Edwards (1972) suggest the name "skeletal elements". They consider "skeletal hyphae" a misnomer, as the term "hyphae" should refer only to multicellular structures. Since septate and therefore multicellular hyphae were observed in the marginal zones of both species, I would advocate retension of Corner's (1953) term "skeletal hyphae".

Skeletal hyphae of the margin are generally smooth, relatively thin-walled with respect to the skeletal hyphae of other regions of the basidiocarp, septate or aseptate hyphae with deeply staining, thin-walled tips. Occasionally, skeletal hyphae in the margin of basidiocarps are arboriform and probably serve in a binding capacity.

Also serving in a binding capacity are skeletal hyphae which develop vertically to the hyphae oriented parallel to basidiocarp growth, 100-500μ from the margin edge. Frequent areas of wall thickening, numerous phlange-like projections, and short solitary, thick-walled branches are characteristics assisting these hyphae in binding together the remaining hyphae.

The colour of the context of both species ranges from pink to vinaceous brown. The context of Fomes roseus may be occasionally faint pink. Weir (1923) considers the intensity of the colour of the context to be of extreme importance in distinguishing these taxa.

Thick-walled, generative hyphae which occur dispersed or in dense masses in the context, are not peculiar to the basidiocarps of Fomes roseus or Fomes cajanderi, as they are found in other

members of the Polyporaceae which have received detailed anatomical study (Corner, 1932b; Van der Westhuizen, 1963; Edwards, 1972; Traquair, 1974).

It is significant that the thin-walled generative hyphae which occur in the context are only present in the vicinity of the margin. Lowe (1957) describes the presence of a small amount of thin-walled, clamped hyphae in the context of Fomes cajanderi, but does not describe their presence in the context of Fomes roseus. Information such as this is misleading, since the presence or absence of this hyphal type and its characteristics are generally given emphasis in the taxonomy of the Polyporaceae (Teixeira, 1960). Also, it is not useful to include descriptions of context hyphae without giving consideration as to where in the context the hyphae described were obtained.

I found growth lines to be consistent features of the context of both species. Bondartsev (1953) and Lowe (1957), referring to these as "zone lines", considered the context of both taxa as "indistinctly zonate". Wong (1973) reports that zone lines in the context of Fomes cajanderi were often observed.

Densely staining, incrusted hyphae and thin-walled chlamydospores only occasionally observed in the context of both taxa are not taxonomically useful features. Neither hyphal modification was reported by Wong (1973) as occurring in the basidiocarp of Fomes cajanderi.

The degree of stratification of the tube layers of basidiocarps of both species is not agreed upon in the literature. Overholts

(1953) describes the tubes of Fomes roseus to be "rather distinctly stratified" and those of Fomes cajanderi as "not definitely stratified". According to Lowe (1957), the tubes of Fomes roseus range from being distinctly to indistinctly stratified, while those of Fomes cajanderi are distinctly stratified. Bondartsev (1953) considered the tube layers of both taxa to be indistinctly layered. Rea (1914) and Weir (1923) state that stratification of the tubes occurs in both taxa. Wong (1973) reports stratification to be a rare occurence in Fomes cajanderi. According to my observations, stratification regularly occurs in the tube layers of both species. It is important to realize that individual tube layers are sometimes obscured by the whitish hyphal plugs in older regions of the tubes and the continuum formed between tube layers. Assuming individual strata to represent annual accretions of growth, stratification would indicate that both taxa are perennial. My personal observations taken over a period of three years, of live basidiocarps of Fomes cajanderi growing in the field, substantiate this statement. Most basidiocarps showed signs of active growth along the margin each growing season.

Hyphal analyses of the dissepiments did not reveal any significant structural differences between the two species. Basidiospore characters and features of the hymenium are traditional sources of diagnostic information. Basidia of Fomes roseus and Fomes cajanderi are unanimously reported to be clavate and cylindrical although there are some slight discrepancies concerning the size of these cells. Characteristics of the basidia of these two species

are not distinctive taxonomic features. The most important microscopic feature encountered in this area of the basidiocarp are the basidiospores. Size and shape differences in the basidiospores have been considered to readily distinguish between these species. Weir (1923), referring to Fomes cajanderi, states that "the rather narrow to ellipsoid to cylindrical hyaline spore has a constant tendency to be allantoid and quite regularly so in occasional specimens. This condition readily distinguishes the species from Fomes roseus, the spores of which never become allantoid, average broader and are frequently acuminate at one end." A "tendency" toward one shape and an "average" breadth greater in the basidiospores of one species cannot be considered to "readily distinguish" between these species any more accurately than the equally variable tendencies in gross basidiocarp morphology. I found the dimensions and shape of basidiospores of each species to overlap to a great degree. Statistical analysis shows that spore size cannot be used to separate these two taxa. The descriptions of Overholts (1953) include ranges in basidiospore breadths which do not at all overlap. He describes the basidiospores of Fomes roseus as 5-7 (-8) X 2.5-3.5μ, elongate-ellipsoid to oblong or short cylindrical, and not at all curved; those of Fomes cajanderi are narrow-cylindric, and slightly curved, 4-7 X 1.5-2μ. Lowe (1957) states that the spores of Fomes roseus are smooth, cylindrical, straight, and 5-8 X 2-3μ; those of Fomes cajanderi are smooth, cylindrical, more or less allantoid, 5-8 X 1.5-2.5μ in size. Basidiospore breadths reported by Bondartsev (1953) also overlap. In

addition, he claims the presence of a slight degree in curvature in the basidiospores of both taxa. Obviously, spore size and shape are far from being the ultimate distinguishing character.

Mounce and Macrae (1937) used spores size differences in setting up mating tests to prove the biological identity of Fomes roseus and Fomes cajanderi (Fomes subroseus (Weir) Overh.). They found a correlation to exist between spore size and patterns of interfertility. Mycelia derived from the narrower spores of Fomes cajanderi were completely intercompatible. Mycelia derived from the broad spores of Fomes roseus were also intercompatible. Monosporous mycelia from the basidiospores of Fomes roseus were consistently incompatible with monosporous mycelia from the narrower spores of Fomes cajanderi. The spore size differences reported by Mounce and Macrae (1937) were not described numerically but displayed graphically using camera lucida drawings. These do not adequately describe the size variations which are encountered in these species.

The conclusion of Mounce and Macrae, that Fomes cajanderi and Fomes roseus are genetically isolated species is supported by Neuhauser and Gilbertson (1971). These authors do not mention size or shape differences in the basidiospores of the two taxa in their publication.

The objections raised to interfertility studies as criteria for the definition of species are mainly of practical concern (Talbot, 1971). Species must be described on the basis of morphology for routine identifications since the classical (and most useful) system of recognizing species is based on morphological

characters. Interfertility tests must be done under cultural conditions with limited numbers of isolates. These limitations must be considered when conclusions are being drawn about species in the field. Talbot states "dikaryotization is only presumptive evidence, but not conclusive proof, that opposed isolates belong to one biological species....From a negative interfertility test, no conclusions can be drawn."

To conclude this section, there is no single morphological feature of the basidiocarp which distinguishes between Fomes roseus and Fomes cajanderi. Common anatomical features underlie variation in the morphology of these taxa and indicate a very close relationship. It is not difficult for the experienced eye to distinguish between the typical forms of these taxa. However, since descriptions must entail a sufficient account of variation within each taxon, morphological concepts become difficult to grasp. Intermediate, young, or unusual forms are impossible to identify with any certainty on the basis of orthodox morphological criteria.

II. Isolates in culture

Cultural studies were done in an attempt to find stable distinguishing features between isolates of Fomes roseus and Fomes cajanderi. Only slight differences were observed between the growth and development of these species in agar and wood cultures.

For isolates on agar, plate coverage required 19 to 22 days for Fomes roseus and 18 to 20 days for Fomes cajanderi. This slight difference in growth rate is not a diagnostically useful

feature, as the amount of overlap in growth rate would prevent accurate identification. Nobles (1965) observed that Fomes roseus required less time to cover a plate than did Fomes cajanderi and considered this difference in growth rate to be a key feature. My results do not support this conclusion.

Snell et al (1928) examined the growth at different temperatures of a number of isolates of Fomes roseus and Fomes cajanderi. They found that Fomes roseus grew more slowly than Fomes cajanderi at all temperatures used. In fact, growth rates of these taxa were so distinctive at 30°C that the authors state that isolates of Fomes cajanderi and Fomes roseus can be distinguished "with absolute reliability" at that temperature. I found that although isolates of Fomes roseus had a tendency to grow more slowly than Fomes cajanderi, this difference was not distinctive for a number of isolates of both taxa. Variability in growth rates of isolates of both species was great at all temperatures, being particularly great at 28°C. At no temperature was growth rate a decisive taxonomic character. The conflicting results of Nobles (1965), Snell et al (1928), and myself is a reflection of the variability in these taxa. It is also an indication that the results of one study are insufficient to make conclusive remarks about taxon characteristics and identity. Considering the variability of the results from studies of growth rate, it is not reasonable to consider growth rates at any temperature a diagnostic feature.

The development of the culture mat of both species is quite similar if not identical. The hyphal types noted in analyses of

field specimens have similar counterparts in the culture mat. No differences in hyphal types, their proportions, or distribution were noted between Fomes roseus or Fomes cajanderi in culture.

Once plate coverage occurs, variations in surface mat characteristics do not allow a distinction to be made between these taxa. Fomes roseus isolates have a tendency to produce a darker colour in the agar medium than Fomes cajanderi. Nobles (1965) observed that Fomes cajanderi did not cause colour changes in the medium, whereas Fomes roseus produced varying intensities of reverse colouration. This is used as a key feature. However, this is not a distinctive character, since isolates of either species may or may not cause reverse colouration.

Extracellular oxidase reactions in response to alcoholic gum guaicum were variable. Nobles also observed this variability in these species and does not use this as a distinctive feature.

In isolates of both species in culture, thin-walled hyphae are consistently clamped. Clamped hyphae may or may not be irregular and thick-walled. Nobles (1965) did not observe clamped hyphae with irregularly thickened walls, or chlamydospores in cultures of Fomes roseus. She did, however, observe these modifications in cultures of Fomes cajanderi. I observed irregular, thick-walled, clamped hyphae and chlamydospores in cultures of both taxa. The occurence of chlamydospores is erratic in both taxa.

Basidiospores produced in culture exhibit the same size tendencies as do spores from natural basidiocarps. Basidiospore size differences are not diagnostic features, as the amount of variation

in this character in both species prevents accurate species designations.

Growth characteristics of the species in and on artificially infected wood were very similar between isolates of Fomes roseus and Fomes cajanderi. However, Fomes roseus generally produced scattered clumps of hyphae on the wood surface while Fomes cajanderi had a tendency to produce a more or less uniform layer of vegetative mycelium over the surface of the wood. This feature, although only a tendency and not always distinctive, might be related to emergence patterns and basidiocarp formation of the two species in nature. Fomes roseus emerges from naturally infected wood usually to form discrete basidiocarps while Fomes cajanderi is known for its propensity to form laterally and vertically fused basidiocarps.

Hyphal development in artificially infected wood was similar to naturally infected wood. Both thin-walled, clamped hyphae and thick-walled hyphae lacking clamps were found growing through the tracheids of artificially and naturally infected wood. Thick-walled hyphae were fewer and hyaline in artificially infected wood, whereas this hyphal type was usually darkly pigmented in naturally infected wood. The similarity of hyphal development of both species in wood must remain inconclusive as it has been found that features of hyphae in wood are not always distinctive even between very different taxa (Traquair, 1974).

Isolates of both species grown on both agar and wood produced octahedral crystals among the surface hyphae.

No substratum preference for wood produced by different species was shown by either Fomes roseus or Fomes cajanderi in culture. Because of this, and since both species have been found on most common wood genera, host preference is not likely directly dependent upon the nutritive or physical characteristics of the wood.

Studies of isolates of Fomes roseus and Fomes cajanderi in agar and wood culture failed to reveal distinguishing characters. Indeed, observations of the development and morphology of these taxa in culture indicate a very close relationship.

III. Chemosystematic studies using thin layer chromatography

Of the six species examined, (Fomes roseus, Fomes cajanderi, Fomes fomentarius, Trametes suaveolens, Fomes pinicola, and Fomes pini) only Trametes suaveolens failed to yield appreciable quantities of ethyl acetate soluble compounds. This might be correlated with the snow white context of the basidiocarp of that species, which would indicate an extreme paucity of pigment components. Further support for this conjecture may be derived from the fact that the pale yellow context hyphae of Fomes pinicola yielded fainter spots on stained, developed chromatograms than did the more deeply coloured context hyphae of Fomes roseus, Fomes cajanderi, Fomes fomentarius, and Fomes pini.

Of the three compounds present in all of the taxa, with the exception of Trametes suaveolens, two are similar in their spectral characteristics to compounds isolated and characterized in Fomes fomentarius by other investigators (Arpin et al, 1974; Arpin,

pers. comm.). Benzotropolone II appears to be closely related to 'fomentariol', a benzotropolone which reportedly comprises 95% of the pigments found in the upper crust of Fomes fomentarius (Arpin et al, in press). Since the spectral data for 'fomentariol' differ somewhat from the spectral data for benzotropolone II, and since 'fomentariol' was isolated from the prominent external layer of the basidiocarp of Fomes fomentarius, and not the context as was benzotropolone II, 'fomentariol' cannot be assumed to be identical to benzotropolone II.

Similarly, spectral analysis of benzotropolone I produced a spectral profile which would indicate that it is related in structure to 'fomentariol' (Appendix V).

The reactions of benzotropolones I and II with indicators I and II are in agreement with this hypothesis concerning their chemical identity. Negative results with indicator II eliminate the possibility of either compound being a phenol, but that they are ring containing compounds is demonstrated by the purple colour produced in response to indicator I.

Arpin et al (in press) have found benzotropolones to occur only in the genus Fomes. However, I am unaware of the range of species investigated by these workers. It is of interest to note that benzotropolones I and II were present in significant amounts in the species traditionally regarded as belonging to Fomes. Thus, chemical data presented here could be interpreted as not supporting modern generic divisions within the genus Fomes. These data might also be interpreted as supporting the identity of the Friesian genus

Trametes as represented by the species T. suaveolens. Trametes, as the genus originally described by Fries, included only species with a pale context.

Phenols I and II are of interest, as they were present in substantial amounts only in Fomes roseus and Fomes cajanderi. Only a trace of phenol I was detected in Fomes pini. These compounds reacted positively with indicators I and II, as did benzotropolone III, but the colours they produced with indicator I were unmistakable in identifying their presence and distinguishing them from other compounds. Phenols I and II have a structure substantially different from benzotropolone III. Their presence in Fomes roseus and Fomes cajanderi is of some taxonomic significance. It is difficult to deny such evidence a prominent place in the classification of these two taxa. Presence of these compounds indicate that Fomes roseus and Fomes cajanderi are chemically quite closely related. These two species exhibit a tube layer and context of a similar rose colour. Possibly this colour is due to the presence of phenols I and II. It would be of some taxonomic significance to dètermine the chemical structure of these compounds.

Fries (1958) reports that cultured material of agaricoid and boletoid fungi produced different spot patterns on chromatograms than those produced by natural material. This was not found to be the case in the work presented here. Chromatograms derived from cultured material of Fomes roseus and Fomes cajanderi were entirely comparable to those from natural material. Fries does not indicate whether or not the cultured material he used had any trace of fruit body

formation of characteristic colouration of the species being cultured. However, discrepancies between my results and those of Fries may be due to differences in taxa and methodology used.

None of the data supports or indicates a closer relationship of Fomes roseus or Fomes cajanderi with the type species of the genera in which they have been placed. In other words, evidence would indicate that a closer relationship exists between Fomes roseus and Fomes cajanderi than between either one of them and other taxa examined in this study.

IV. Summary and conclusion

Criteria for the circumscription of Fomes roseus and Fomes cajanderi are derived from two categories: variable and stable sources of characteristics. The first category includes gross basidiocarp morphology, host preference, spore size, growth rate, and gross characteristics of the culture mat. The second includes the hyphal anatomy of field specimens and isolates in culture, rot characteristics, and chemical characters. Basidiocarp morphology of these taxa, though by necessity regarded as the prime source of taxonomic characters, is frequently not sufficient for making a distinction between these taxa. Basidiocarp morphology of both taxa is however, based on a common and fundamental hyphal anatomy. Variation in the appearance of field specimens can be attributed to two main factors. First, environmentally induced variations in the pattern and intensity of pigment deposition between the hyphae of the basidiocarp cause a bewildering range of colouration and texture. Second, emergence patterns of mycelium from wood substrata,

coupled with the effects of the environment, produce wide variations in basidiocarp shape. The variations in colour and shape are responsible for the confusion in the literature regarding the specific nature of these taxa.

Cultural studies fail as a source of characters in distinguishing between these taxa. The key morphological characters in distinguishing Fomes roseus and Fomes cajanderi discussed by Nobles (1965) are much more variable than originally supposed. Growth rate of isolates of the two taxa in culture is not a diagnostic feature at any temperature. Host range, considered to be distinctive to a small extent (Weir, 1923) for these species is not demonstrated by either field specimens or isolates in culture.

Basidiospore sizes for Fomes roseus and Fomes cajanderi do not exhibit a statistically significant difference and consequently cannot be considered an ultimate diagnostic feature (Overholts, 1953).

Interfertility tests are not only impractical, but are inconclusive when negative (Talbot, 1971).

Stable characters are indicative of an extremely close relationship between these taxa. Hyphal anatomy of field specimens and culture mats of isolates of these species is extremely uniform. Occasional variation in hyphal anatomy of specimens in vivo and in vitro are not apparently correlated with other taxonomic features used in distinguishing Fomes roseus and Fomes cajanderi and consequently are given no taxonomic weight.

Both taxa produce a dry brown cubical rot of naturally and

artificially infected wood. The differences in the rot characteristics of each species observed by Weir (1923) were not observed during this study.

Chemical characters do not support a particularly close relationship between either Fomes roseus or Fomes cajanderi and the type species of the genera in which they have been placed. Chemical characters do support data from morphological and anatomical studies in indicating that these species are very closely related.

A practical approach to this problem in species delimitation would be to place both taxa in one species as has indeed been done by a number of investigators (Murrill, 1903; Bresadola, 1911, cited in Bondartsev, 1953; Imazeki and Tsuguo, 1965). The name Fomes roseus (Alb. & Schw. ex Fries) Cooke was published in 1885 and consequently has priority over the name Fomes cajanderi Karst. which was not published until 1904. Fomes roseus (Alb. & Schw. ex Fries) Cooke is circumscribed as follows.

> 'In field specimens, basidiocarp primordia pulvinate, 2.0-7.0 mm in diameter, pink to vinaceous; the mature basidiocarp sessile or effused-reflexed, rarely resupinate, applanate to ungulate, leathery to corky, to hard and rigid, pink to vinaceous brown at first, remaining so on the margins of vigorous specimens, becoming reddish-brown or gray to black; young specimens minutely tomentose, becoming glabrous or somewhat fibrilose; the pileus surface rippled to hummocky, more or less incrusted, zonation apparent or obscured; the margin sterile, obtuse or acute; context fibrous to corky, rose or vinaceous brown with conspicuous darker growth lines; pores concolorous with the context or somewhat lighter, circular or subangular, daedeloid on effused portions, averaging 3-6/mm; tubes stratified.
>
> Hyphae in tracheids of naturally and artificially infected wood of two types: thin-walled clamped hyphae and thick-walled, hyaline to pigmented hyphae. In mature basidiocarps, young regions of the context with clamped,

thin-walled, regular to thick-walled, irregular generative hyphae and thick-walled skeletal hyphae; chlamydospores globose to fusiform, infrequent; pileus surface a palisade of thick-walled skeletal hyphae embedded in a reddish brown amorphous agglutinating substance; basidia clavate, cylindrical, 4.2-6.3 X 13-17μ; basidiospores narrow, cylindrical, hyaline, with or without a slight curve above the hilar apiculus, 4.5-7.5 X 1.7-3.2μ.

Most isolates fruit readily in agar and wood culture; on agar, mycelial mats pale or rose coloured; pores round to angular; reverse colouration absent or reddish brown; extracellular oxidase variable; basidia clavate, 5.2-8.1 X 14-20μ; basidiospores smooth, narrow, cylindrical, with or without a slight curve above the hilar apiculus, 4.0-8.0 X 1.7-3.1μ; fibre hyphae of two types: thick-walled, generally hyaline, smooth, regular and flexuous hyphae; and contorted and irregular hyphae; the lumen of both types generally thin or occluded; nodose-septate hyphae of two types: thin-walled, abundantly clamped, branched hyphae; and thick-walled hyphae, having an irregular, sinuous lumen; chlamydospores thin-walled to fusiform 13-20 X 5-20μ, infrequent.

With reference to work reported here, phenolic compounds I and II unique to field specimens and isolates in culture.

Produces a reddish brown cubical rot of coniferous wood, especially that of Picea, but also Abies, Juniperus, Larix, Pinus, Pseudotsuga and Tsuga; occasionally found on hardwoods such as Betula, Populus and Prunus.

Widely distributed through the northern hemisphere.'

Table 1. Characteristics of 2 phenol compounds and 3 benzotropolones isolated from Fomes roseus (Alb. & Schw. ex Fries) Cooke and Fomes cajanderi Karst.

Legend

-	no apparent reaction
(+)	faint visible reaction
+	strong visible reaction
*	underscored numbers represent wavelengths where peaks occurred on the Spectrogram (Appendix IV)
**	numbers with 'S' following indicate the location of shoulders on the flanks of major peaks (Appendix IV)

Table 1

Compound	Rf(X100) in Solvent A	Rf(X100) in Solvent B	Fluorescence with UV light	Reaction with Indicator I	Reaction with Indicator II	Spectral Data (nm)
Benzotropolone I	45		pale yellow-green	purple	-	208*, 274, 330
Benzotropolone II	82		bright green	purple	-	210S**, 220, 274
Benzotropolone III	75		faint yellow	purple	(+)	210S, 227, 274, 282S
Phenol I		72	-	violet	+	210S, 222, 254S
Phenol II		80	-	indigo	+	210, 258S, 274

Table 2. Distribution of 2 phenol compounds and 3 benzotropolones present in the ethyl acetate fractions of ground mycelium of 5 wood decay fungi

Legend

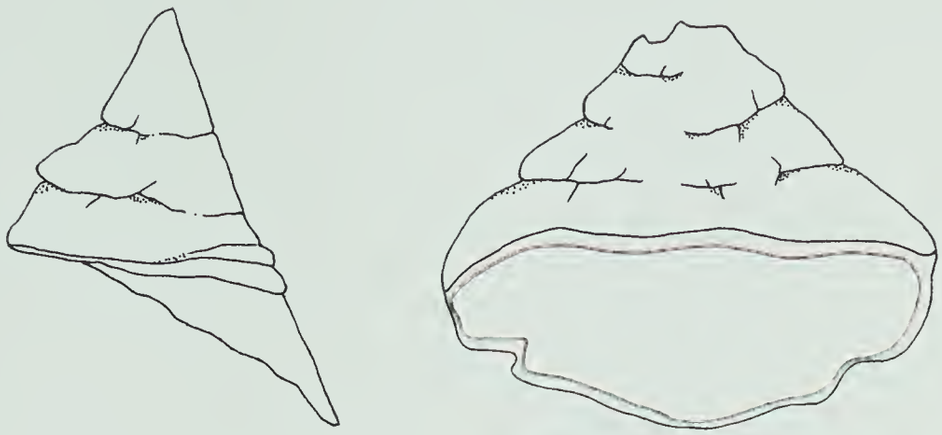
-	no detectable amount
tr	trace amount
+	small amount
++	easily detectable amount
*	includes natural basidiocarps and cultured material

Table 2

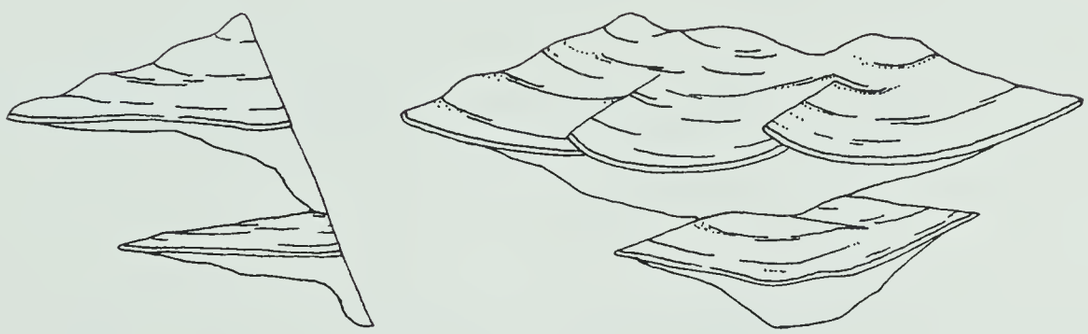
Species	No. of specimens examined*	Compounds Observed				
		Benzotropolone I	Benzotropolone II	Benzotropolone III	Phenol I	Phenol II
Fomes roseus (Alb. & Schw. ex Fries) Cooke	8	++	++	++	++	++
Fomes cajanderi Karst.	10	++	++	++	++	++
Fomes fomentarius (L. ex Fries) Kickx	2	++	++	++	-	-
Fomes pinicola (Swartz ex Fries) Cooke	1	+	+	+	-	-
Fomes pini (Thore ex Fries) Karst.	1	++	++	++	+	-
Trametes suaveolens (L. ex Fries) Fries	1	tr	-	-	-	-

Figure 1. Solitary, ungulate basidiocarp of Fomes roseus (Alb. & Schw. ex Fries) Cooke
Actual size

Figure 2. Applanate, laterally and vertically fused pilei of Fomes cajanderi Karst.
Actual size



1



2

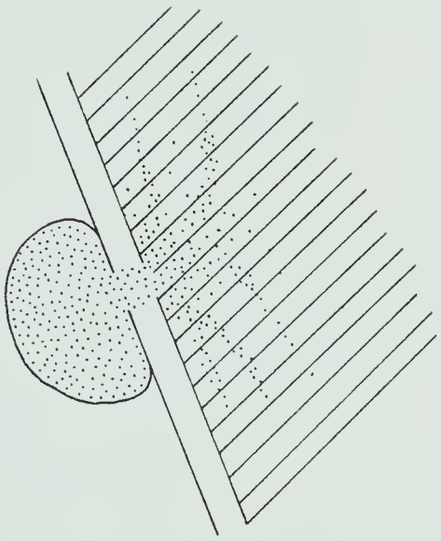
Figure 3. Pulvinate basidiocarp primordium of Fomes roseus (Alb. & Schw. ex Fries) Cooke closely appressed to the surface of the substratum

X 10

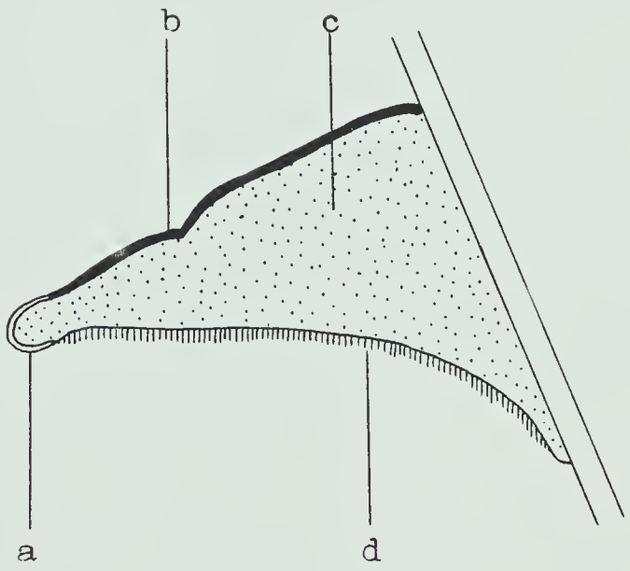
Figure 4. Regions of the mature basidiocarp of Fomes roseus (Alb. & Schw. ex Fries) Cooke

a -margin
b -pileus surface
c -context
d -dissepiments

X 1.3



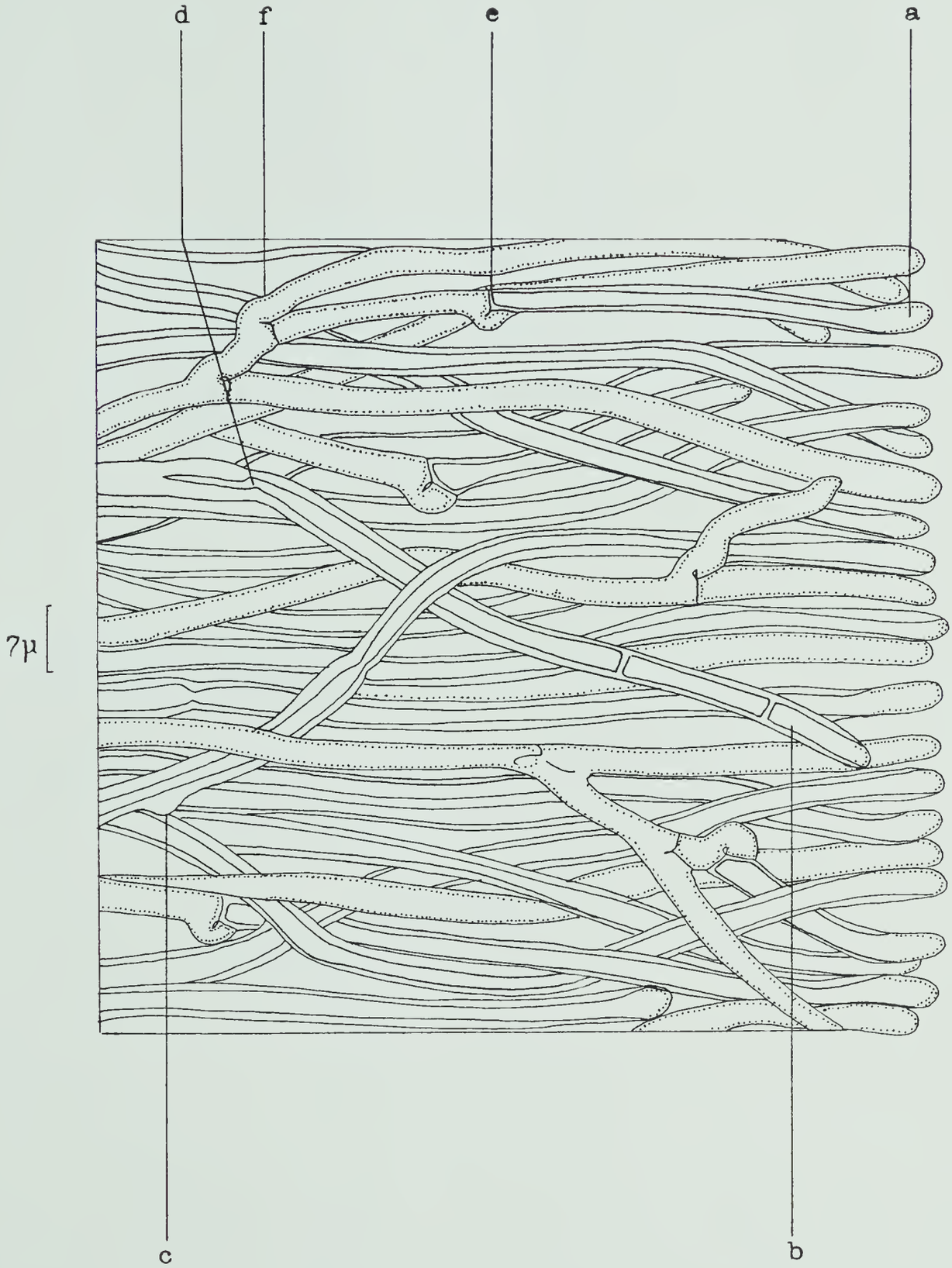
3



4

Figure 5. Organization of hyphae of the margin of a basidiocarp of *Fomes roseus* (Alb. & Schw. *ex* Fries) Cooke

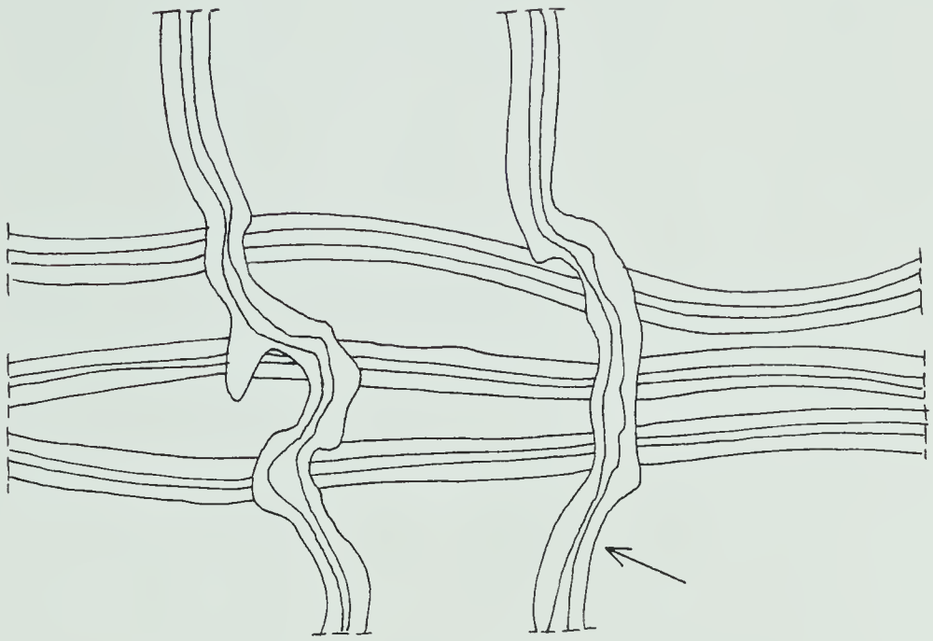
a -smooth, rounded, thin-walled apex of a skeletal hypha
b -septa in the thin-walled terminal region of a skeletal hypha
c -asymmetric, phlange-like projection on a skeletal hypha
d -constriction in a skeletal hypha
e -skeletal hypha originating from a clamp connexion
f -clamp connexion serving as a point of origin for a lateral branch



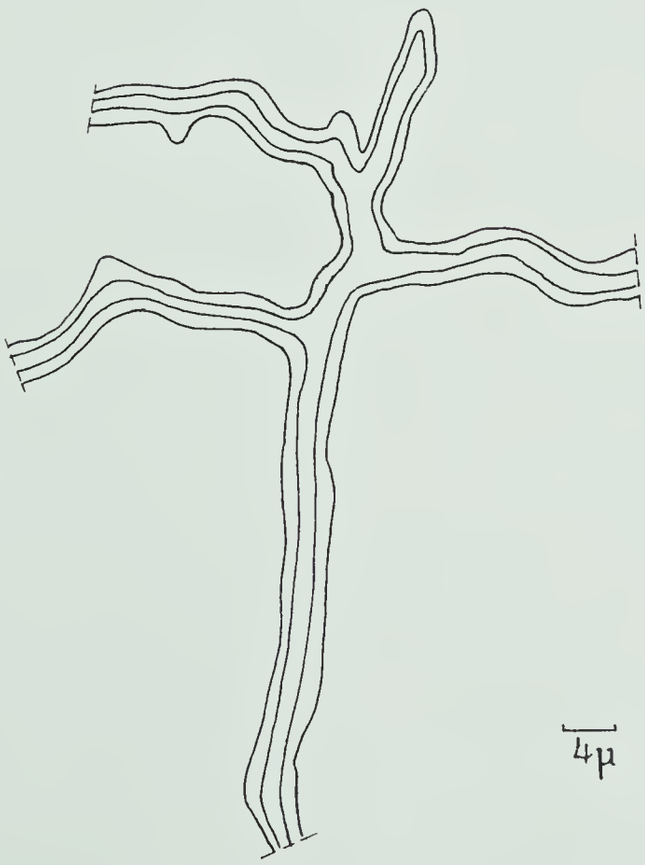
5

Figure 6. Skeletal hyphae (arrow) oriented perpendicular to direction of growth in the margin of the basidiocarp of Fomes roseus (Alb. & Schw. ex Fries) Cooke

Figure 7. Lateral branching of the apical region of a skeletal hypha of Fomes roseus (Alb. & Schw. ex Fries) Cooke

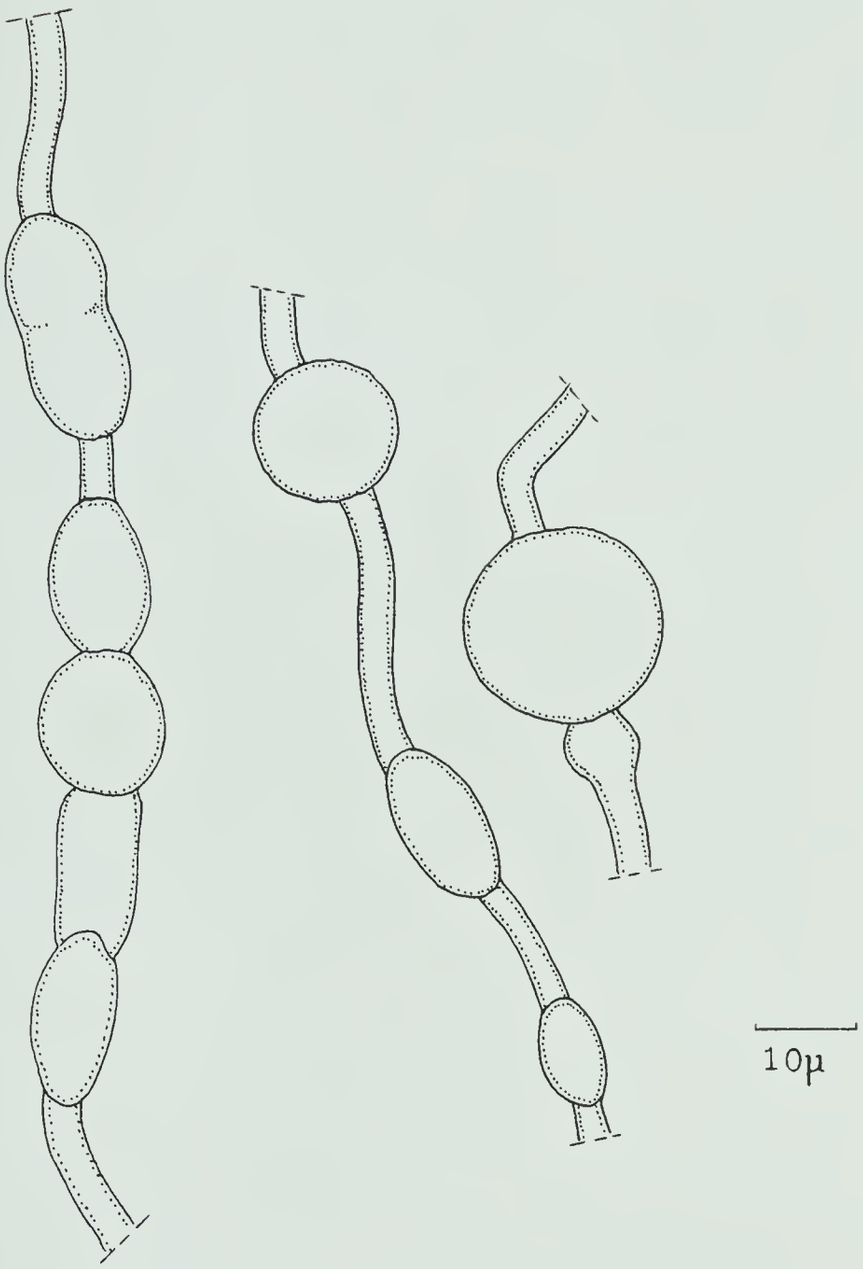


6



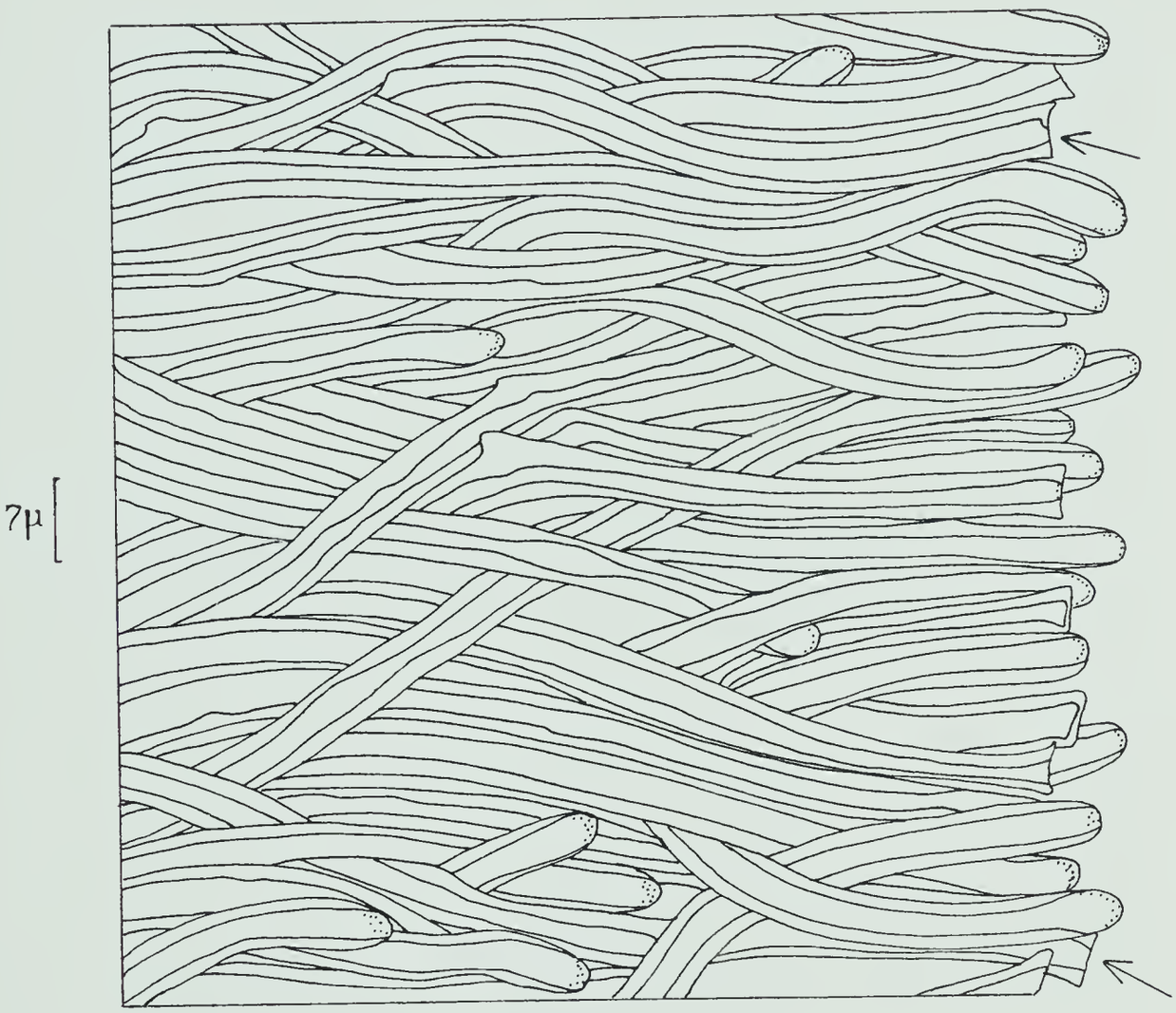
7

Figure 8. Thin-walled, globose to fusiform chlamydospores in linear series on thin-walled hyphae located 200-400μ from the margin edge of Fomes roseus (Alb. & Schw. ex Fries) Cooke



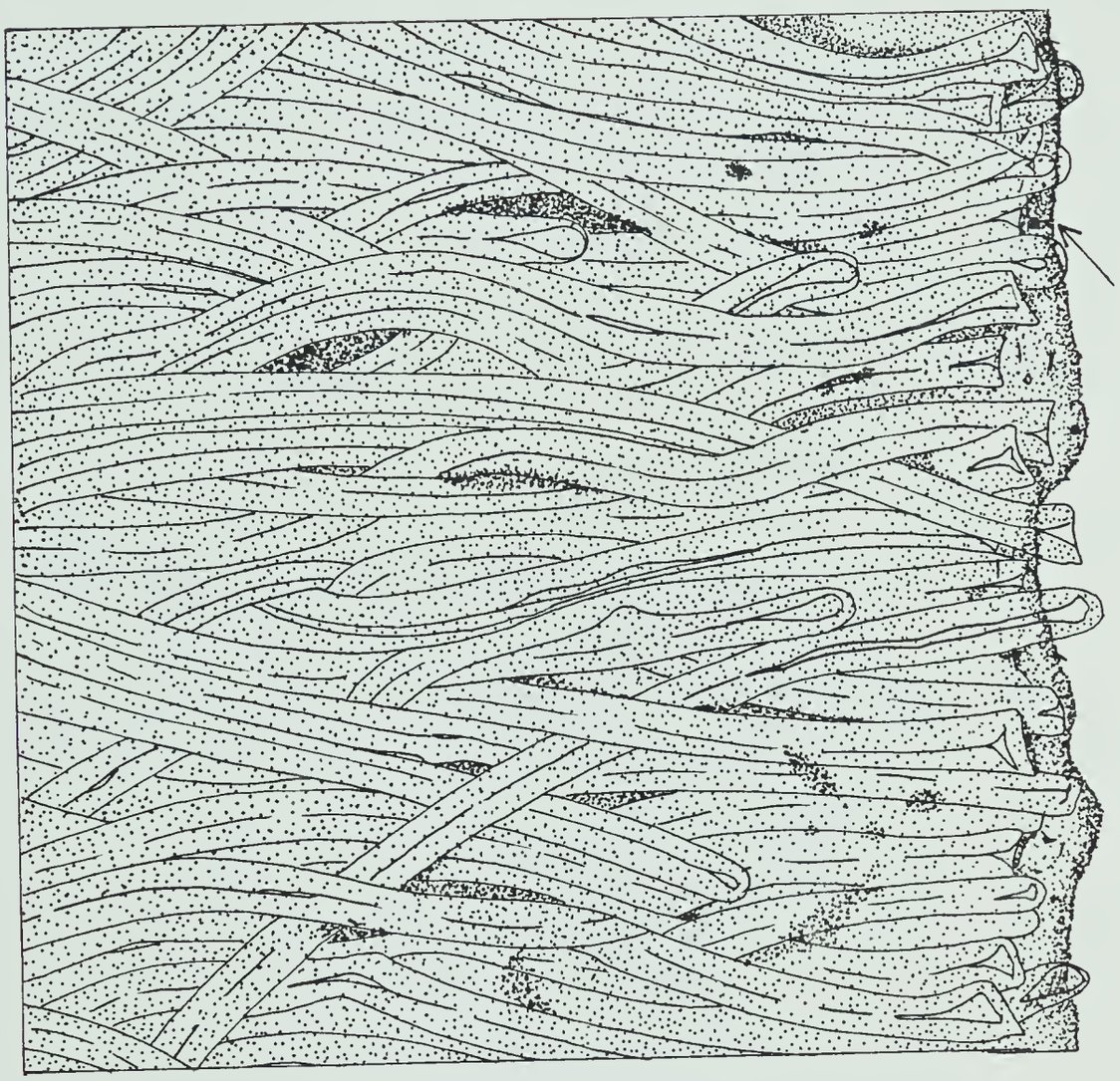
8

Figure 9. Hyphal organization of the pileus surface of *Fomes roseus* (Alb. & Schw. *ex* Fries) Cooke
Note truncated hyphae (arrows)



9

Figure 10. Hyphal organization of incrusted pileus surface of *Fomes roseus* (Alb. & Schw. *ex* Fries) Cooke
Note deposits of amorphous, agglutinating substance (arrow)

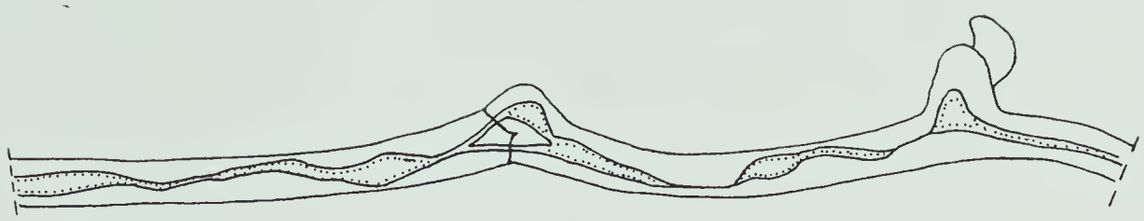


10

Figure 11. Brittle, thick-walled, clamped hypha from the context of Fomes roseus (Alb. & Schw. ex Fries Cooke

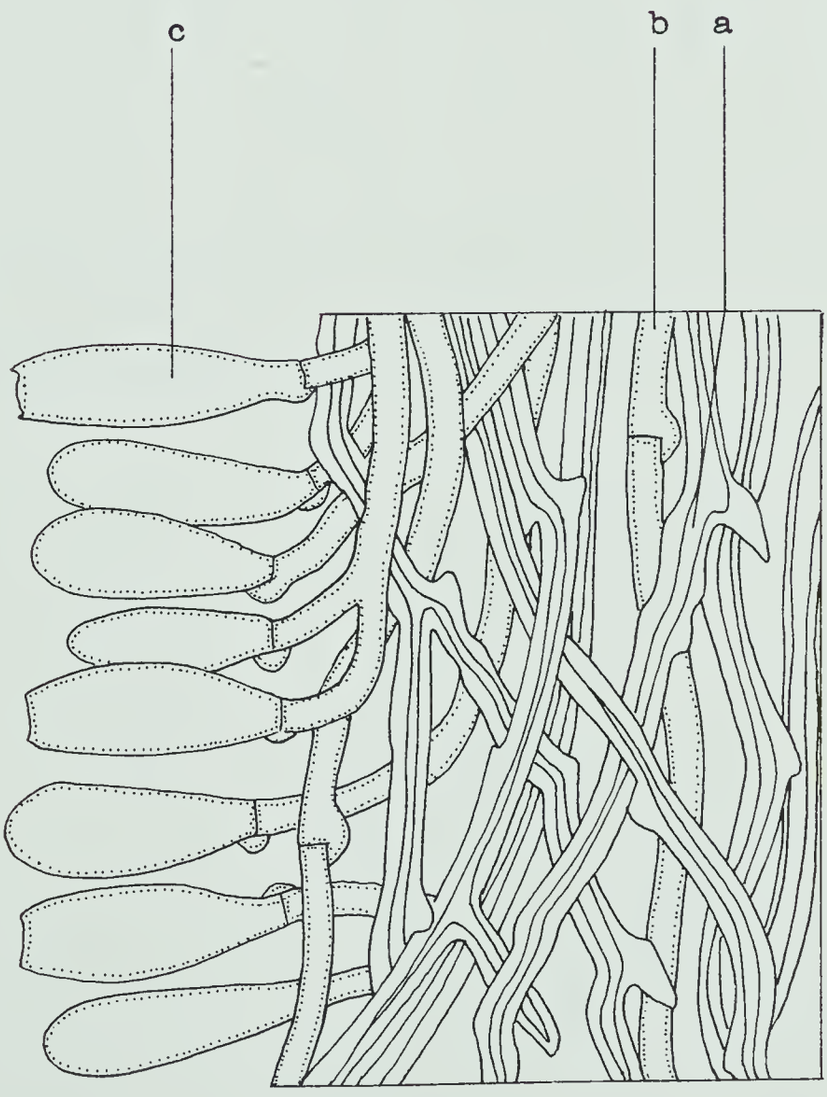
Figure 12. Hyphal organization of dissepiments of Fomes roseus (Alb. & Schw. ex Fries) Cooke showing basidial palisade

a -contorted, knobby skeletal hypha
b -generative hypha
c -basidium



3.5μ

11

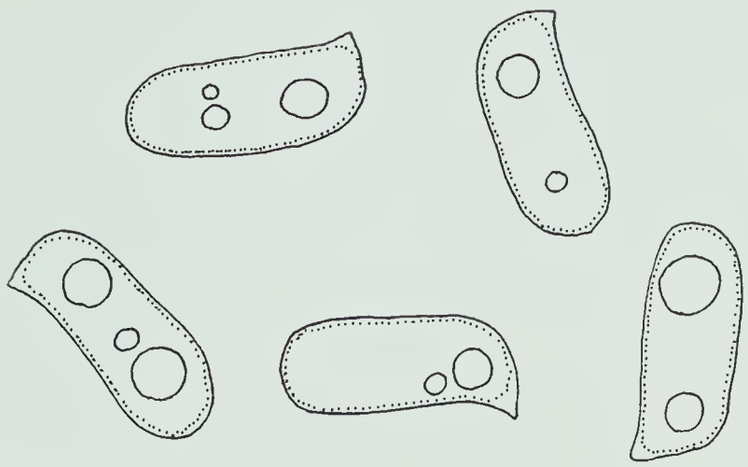


6μ

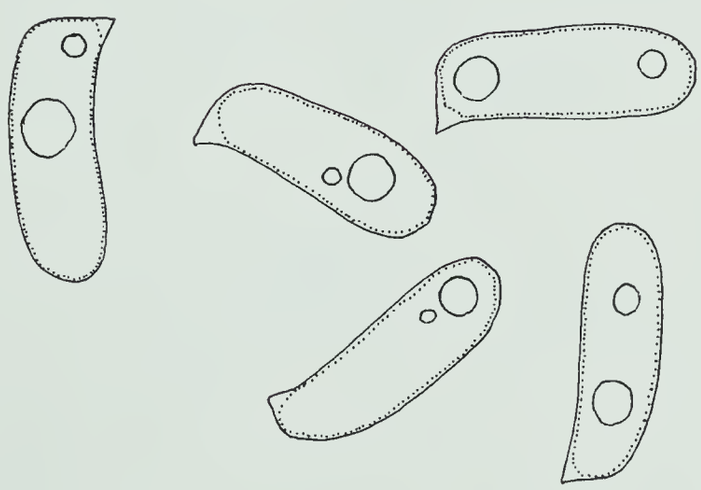
12

Figure 13. (a) Basidiospores of Fomes roseus (Alb. & Schw. ex Fries) Cooke

(b) Basidiospores of Fomes cajanderi Karst.



13a

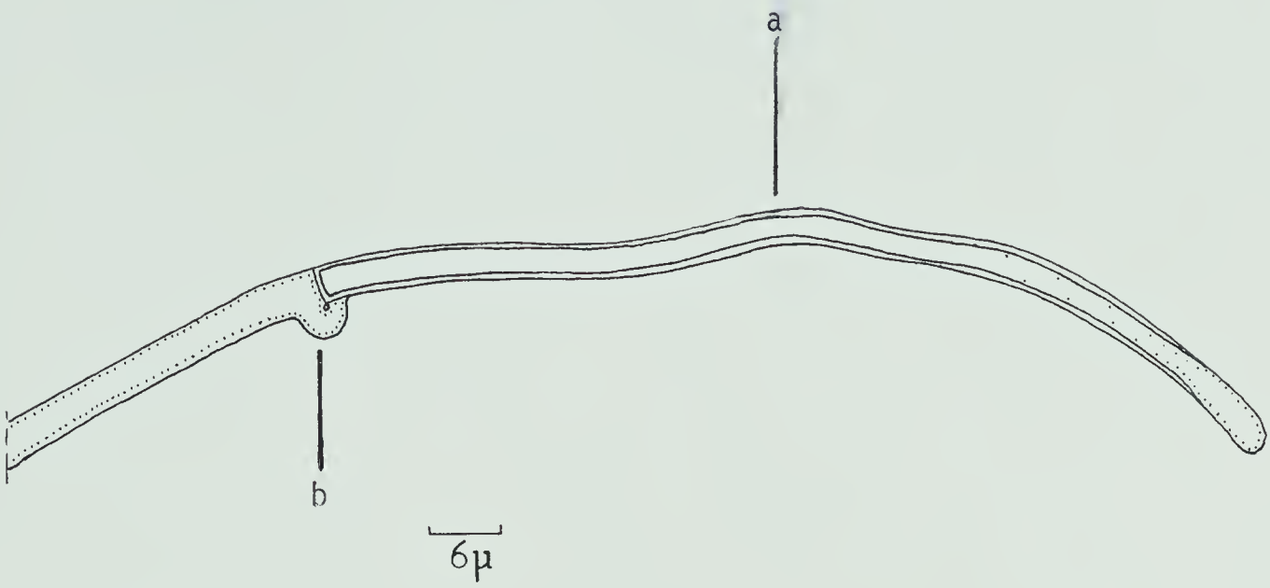


2μ

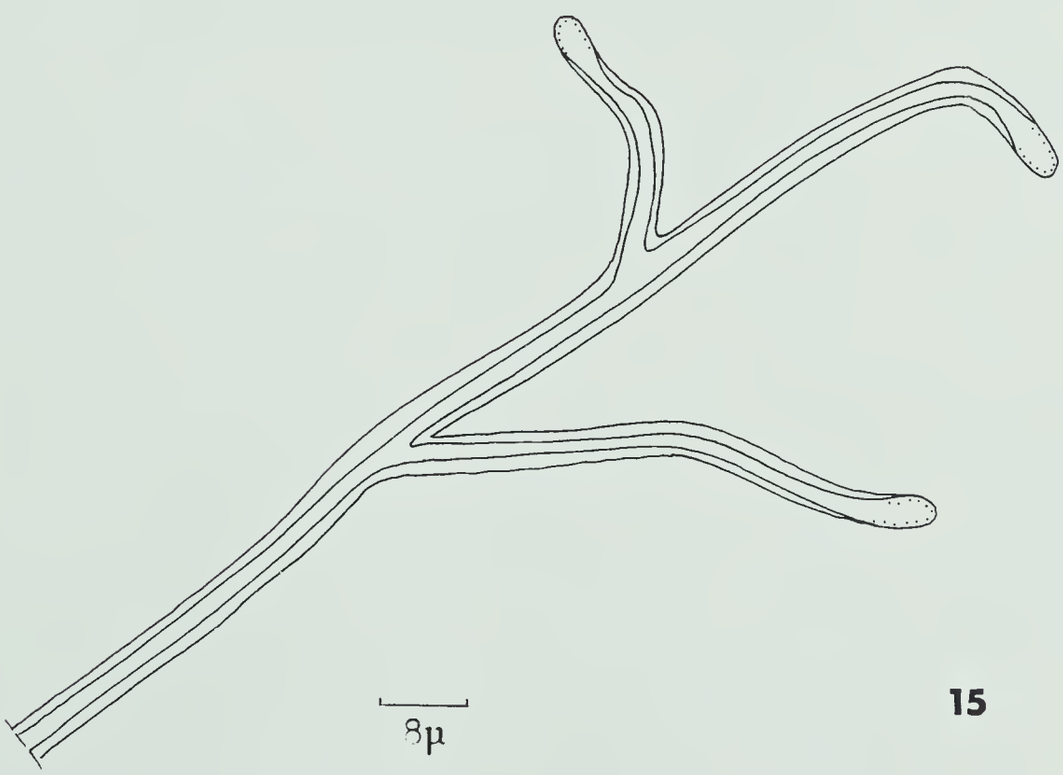
13b

Figure 14. A young fibre hypha (a) subtended by a clamp connexion (b) from the margin of the mycelial mat of Fomes roseus (Alb. & Schw. ex Fries) Cooke

Figure 15. Fibre hypha with apical branching from the mycelial mat of Fomes roseus (Alb. & Schw. ex Fries) Cooke



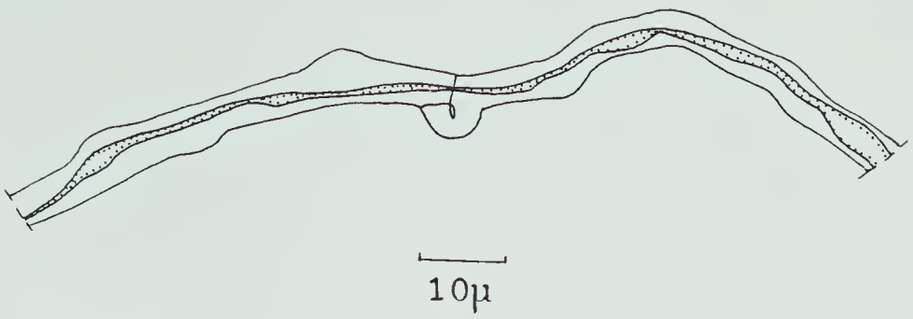
14



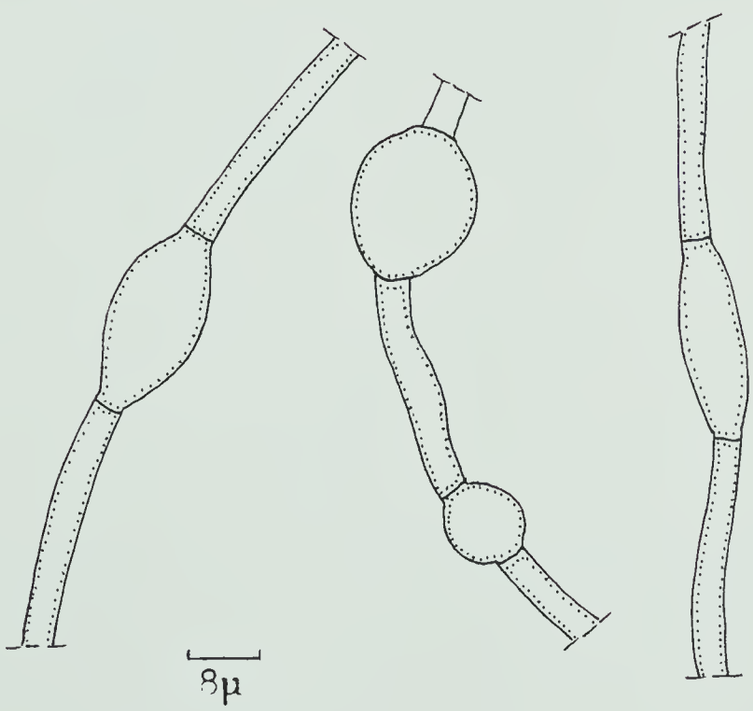
15

Figure 16. Irregular, thick-walled nodose-septate hypha from the mycelial mat of Fomes roseus (Alb. & Schw. ex Fries) Cooke

Figure 17. Thin-walled chlamydospores of Fomes roseus (Alb. & Schw. ex Fries) Cooke which form beneath the surface of agar



16

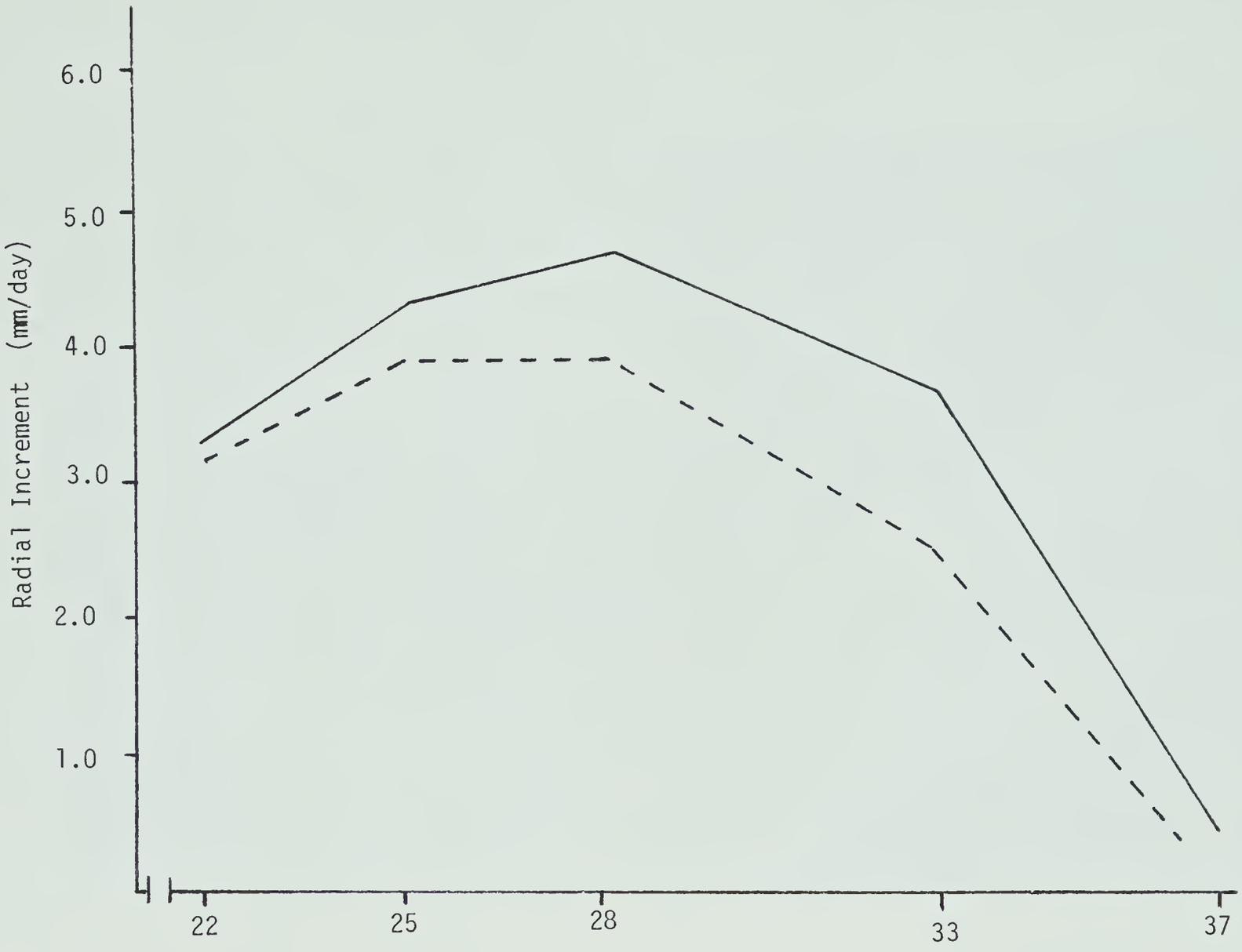


17

Figure 18. Effect of temperature on growth rate of vegetative mycelium of Fomes roseus (Alb. & Schw. ex Fries) Cooke and Fomes cajanderi Karst.

——— growth rate of Fomes roseus

------ growth rate of Fomes cajanderi



18

Plate 1a. Thick-walled hyphae of Fomes roseus (Alb. & Schw. ex Fries) Cooke in the tracheids of macerated spruce.
Phase contrast microscopy
X 620

Plate 1b. Thick-walled skeletal hyphae of the context of Fomes roseus (Alb. & Schw. ex Fries) Cooke
Note the phlange-like projection (arrow)
Light field microscopy
X 920

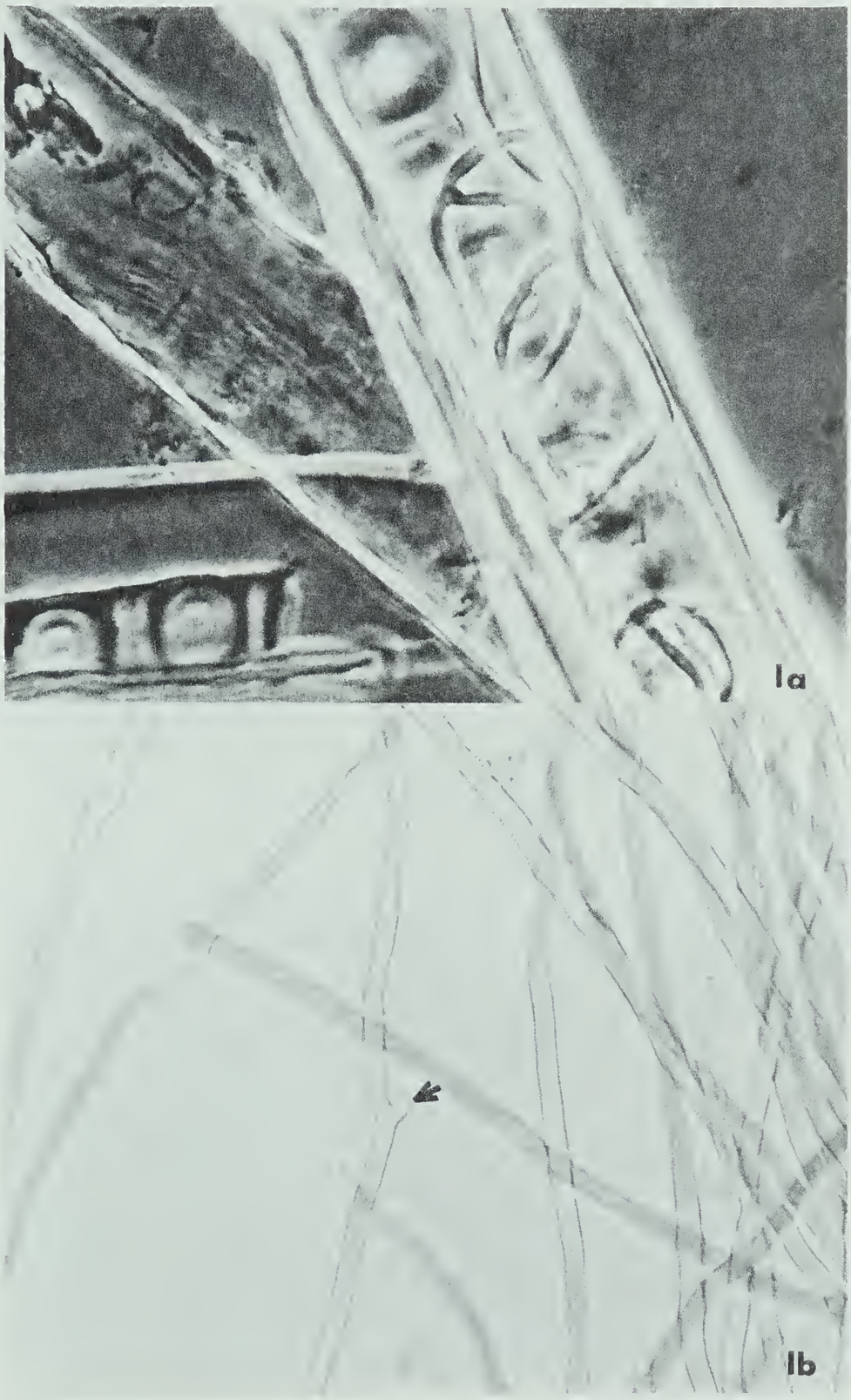
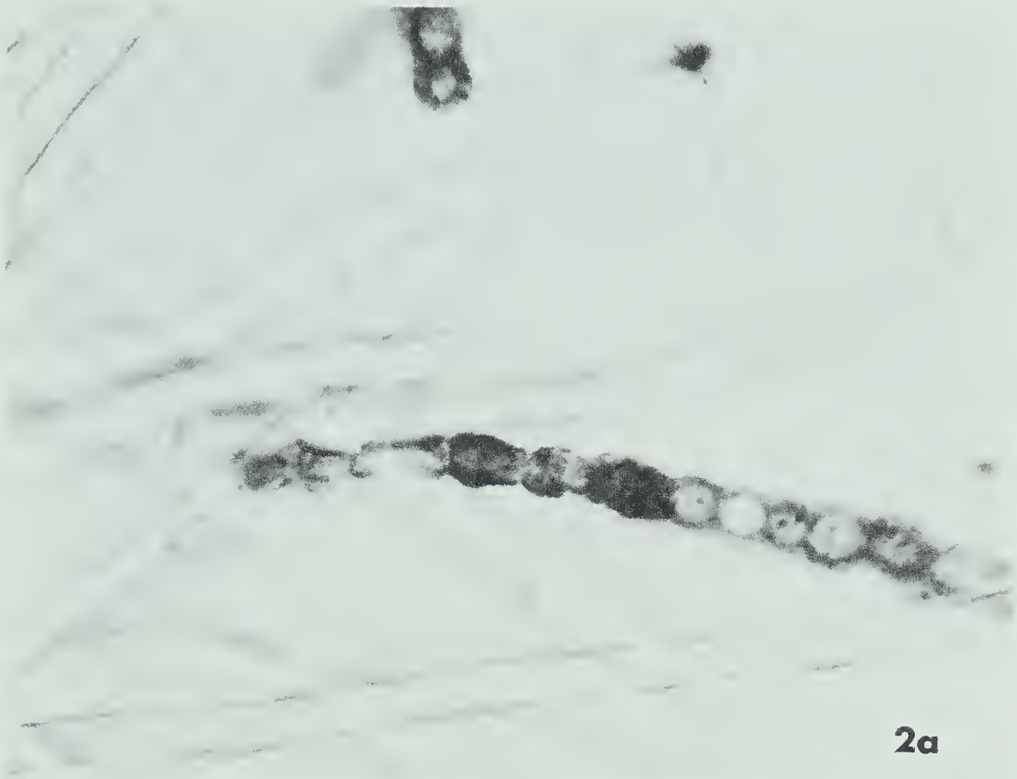
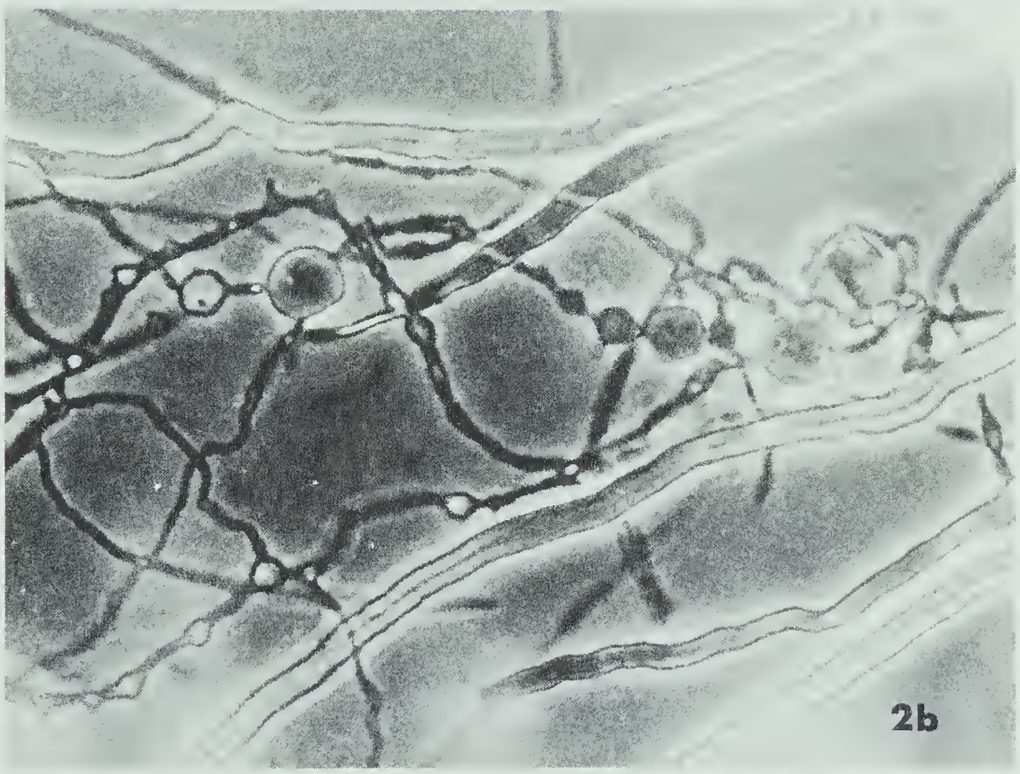

Ia
Ib

Plate 2a. Chlamydospores in linear series from the margin of *Fomes roseus* (Alb. & Schw. *ex* Fries) Cooke
Light field microscopy
X 1000

Plate 2b. Globose chlamydospores from the margin of *Fomes roseus* (Alb. & Schw. *ex* Fries) Cooke
Phase contrast microscopy
X 920



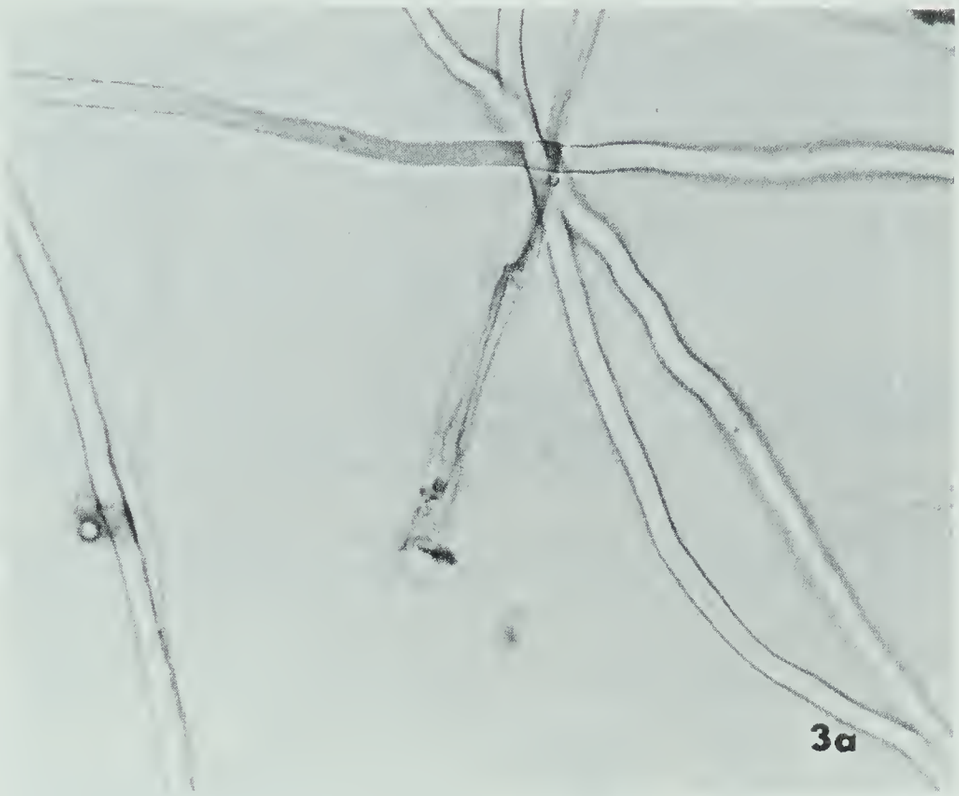
2a



2b

Plate 3a. A thick-walled, brittle generative hypha (arrow) from the context of Fomes roseus (Alb. & Schw. ex Fries) Cooke
Note the sinuous lumen
Light field microscopy
X 820

Plate 3b. A thick-walled generative hypha from the context of Fomes roseus (Alb. & Schw. ex Fries) Cooke
Light field microscopy
X 950



3a

3b

BIBLIOGRAPHY

ADAMS, D.H. and L.H. ROTH. 1967. Demarcation lines in paired cultures of Fomes cajanderi as a basis for detecting genetically distinct mycelia. Can. J. Bot. 45: 1583-1589.

ADAMS, D.H. and L.H. ROTH. 1969. Intraspecific competition among genotypes of Fomes cajanderi. Forest Sci. 15: 327-331.

AHMAD, S.S. and P. MILES. 1970. Hyphal fusions in Schizophyllum cummune. 2. Effects of environmental and chemical factors. Mycologia 62: 1008-1017.

AINSWORTH, G.C. and P.H.A. SNEATH. 1962. Microbial Classification. Cambridge University Press, London.

AMES, A. 1913. A consideration of structure in relation to genera of the Polyporaceae. Annls mycol. 11: 211-253.

ANDERSON, N.A., S.S. WONG and J.W. SCHWANDT. 1973. The Pleurotus ostreatus-sapidus species complex. Mycologia 65: 28-35.

ARPIN, N. 1977. Personal communication.

ARPIN, N. et J. FAVRE-BONVIN. In press. Les pigments du polypore Fomes fomentarius (L. ex Fr.) Kickx. Bull. Soc. mycol. Fr.

ARPIN. N., J. FAVRE-BONVIN and W. STEGLICH. 1974. Le fomentariol: nouvelle benzotropolone isolée de Fomes fomentarius. Phytochemistry 13: 1949-1952.

ARPIN, N. and J. FIASSON. 1971. The pigments of basidiomycetes: their chemotaxonomic interest. In: Evolution in the Higher Basidiomycetes. Edited by: R. Peterson, University of Tennessee Press, Knoxville. pp. 63-98.

AUSTWICK, P.K.C. 1968. Effects of adjustment to the environment on fungal form. In: The Fungi Vol. III. Edited by: G.C. Ainsworth and A.S. Sussman, Academic Press Inc., New York. pp. 419-445.

BALLAL, S.K. 1967. Certain cultural and physiological variations among some resupinate polypores. J. Tenn. Acad. Sci. 42: 97-103.

BENEDICT, R.G. and L.R. BRADY. 1969. Metabolic and taxonomic

considerations of selected higher fungi. In: Fermentations Advances. Edited by: D. Perlman, Academic Press, Inc., New York.

BIGGS, R. 1937. The species concept in Corticium coronilla. Mycologia 29: 686-705.

BIKKINSHAW, J.H. 1965. Chemical constituents of the fungal cell. 2. Special chemical products. In: The Fungi Vol. I. Edited by: G.C. Ainsworth and A.S. Sussman, Academic Press Inc., New York. pp. 179-228.

BONDARTSEV, A. 1953. The Polyporaceae of the European U.S.S.R. and Caucasia. Translated from Russian by: Israel Program for Scientific Translations, Jerusalem. 1971.

BONDARTSEV, A. and R. SINGER. 1941. Zur Systematik der Polyporaceen. Annls mycol. 39: 43-65.

BONDARTSEVA, M.A. 1961. A critical review of the most recent classifications of the family Polyporaceae. Botanicheskii zhurnal SSSR. 46: 587-593. (Translation 7325C, Canada Dept. Agriculture).

BONNET, J.L. 1959. Application de la chromatography sur papier a l'étude divers champignons (Basidiomycetes-Hymenomycetes). Bul. Soc. mycol. Fr. 75: 215-352.

BOSE, S.R. 1941. The nature of the colouring substances in coloured Polyporaceae. Trans. natn. Inst. Sci. India 2: 69-86.

BOYCE, J.S. 1923. A study of decay in Douglas fir in the Pacific Northwest. Bull. U.S. Dep. Agric. 1163.

BURGESS, A. 1955. Problems associated with the species concept in Mycology. In: Species Studies in the British Flora. Edited by: J.E. Lousely, T. Buncle & Co., Arbroath. pp. 65-82.

BUTLER, G.M. 1968. Environmentally induced changes in clamp connection incidence in hyphal branching systems of Coprinus disseminatus. Ann. Bot. (N.S.) 32: 847-862.

CARTWRIGHT, K.ST.G. and W.P.K. FINDLAY. 1958. Decay of Timber and its Prevention. 2nd ed. H.M.S.O., London.

CHILDS, T.W. 1937. Variability of Polyporus schweinitzii in culture. Phytopathology 27: 29-50.

CIFERRI, R. 1932. The criteria for the definition of species in mycology. Annls mycol. 30: 122-136.

COOKE, W.B. 1959. The genera of pore fungi. Lloydia 22: 163-207.

CORNER, E.J.H. 1932a. The friut body of Polystictus xanthopus. Ann. Bot. (London) 46: 71-111.

CORNER, E.J.H. 1932b. A Fomes with two systems of hyphae. Trans. Brit. mycol. Soc. 17: 51-81.

CORNER, E.J.H. 1953. The construction of polypores. I. Introduction: Polyporus sulphureus, P. squamosus, P. betulinus and Polystictus microcyclus. Phytomorphology 3: 152-167.

COWLING, E.B. and A. KELMAN. 1964. Influence of temperature on growth of Fomes annosus isolates. Phytopathology 54: 373-378.

CUNNINGHAM, G.H. 1946. Notes on the classification of the Polyporaceae. N.Z. J. Sci. Technol. 28: 238-251.

CUNNINGHAM, G.H. 1954. Hyphal systems as aids in identification of species and genera of the Polyporaceae. Trans. Brit. mycol. Soc. 37: 44-50.

CUNNINGHAM, G.H. 1965. The Polyporaceae of New Zealand. Bull. N.Z. Dep. scient. ind. Res. 164.

DAVIS, P.H. and V.H. HEYWOOD. 1973. Principles of Angiosperm Taxonomy. Robert E. Krieger Publishing Co., Huntington, New York.

DONK, M.A. 1960. The generic names proposed for the Polyporaceae. Persoonia 1: 173-302.

DONK, M.A. 1971. Multiple convergence in the polyporaceous fungi. In: Evolution in the Higher Basidiomycetes. Edited by: R. Peterson, University of Tennessee Press, Knoxville. pp. 393-422.

EDWARDS, R.G.W. 1972. A biosystematic study of Coriolus hirsutus (Fr.) Quélet and Coriolus pubescens(Fr.) Quélet. Ph.D. thesis, University of Alberta, Edmonton.

ERIKSSON, J. 1958. Studies in the Heterobasidiomycetes and Homobasidiomycetes -Aphyllophorales of Mudus National Park in Northern Sweden. Symb. bot. Upsal. 16: 1-172.

FARO, S. 1972. Physiological aspects of pigment production in relation to morphogenesis in Panus tigrinus. Mycologia 64: 375-387.

FAVRE-BONVIN, J., N. ARPIN and J. GRIPENBERG. 1977. Sur

l'anhydrofomentariol, nouveau pigment de Fomes fomentarius. Phytochemistry 16: 495-496.

FRIES, E. 1874. Hymenomycetes Europaei sive epicriseos systematis mycologici. Editio altera. Scripsit Elias Fries. A. Asher, Amsterdan, 1963.

FRIES, N. 1958. Paper chromatography as a diagnostic aid in Hymenomycetes. K. VetenskSamh. Upps. Arsb. 2: 5-16.

FRITZ, C. 1923. Cultural criteria for the distinction of wood-destroying fungi. Trans. R. Soc. Can. 17: 191-288.

GOLOVIN, P.N. 1958. The idea of species in mycology. In: The Species Problem in Botany. Acad. Sci. U.S.S.R., Moscow. (Translation 65989, Canada Dept. Agriculture).

GUZMAN, G. 1973. Some distributional relationships between Mexican and U.S. mycofloras. Mycologia 65: 1319-1330.

HANSEN, L. 1958. On the anatomy of the Danish species of Ganoderma. Bot. Tidsskr. 54: 333-352.

HUBERT, E.E. 1924. The diagnosis of decay in wood. J. agric. Res. 29: 523-567.

IMAZEKI, R. and H. TSUGUO. 1965. Coloured Illustrations of Fungi of Japan. 20, 1-Chome Uchikyuhojimachi Higashiku, Osaka, Japan.

ITO, Y., Y. NOZAWA and T. YONEYA. 1968. Pigment patterns of dermatophytes on thin layer chromatograms. J. Chromatogr. 35: 573-575.

KARSTEN, P.A. 1903. Fungi novi, paucis exceptis, in Siberia a clarissimo O.A.F. Loennbohm collecti. Ofvers, finska VetenskSoc. Forh. 46: 1-9.

KENNEDY, L.L. and R.J. LARCADE. 1971. Basidiocarp development in Polyporus adustus. Mycologia 63: 69-78.

KIRK, T.K., L.F. LORENZ and M.S. LARSEN. 1975. Partial characterization of a phenolic pigment from sporocarps of Phellinus igniarius. Phytochemistry 14: 281-284.

KORSTIAN, C.F. and W.D. BRUSH. 1931. Southern white cedar. Tech. Bull. U.S. Dep. Agric. 251.

LANGE, M. 1952. Species concept in the genus Coprinus. Dansk bot. Ark. 14: 1-164.

LARCADE, R.J. 1970. Development of Polyporus adustus Fries and the influence of microenvironment. Ph.D. thesis, University of Alberta, Edmonton.

LOHWAG, K. 1940. Zur Anatomie des Deckgeflechtes der Polyporaceen. Annls mycol. 38: 401-451.

LOWE, J.L. 1956. Type studies of the Polypores described by Karsten. Mycologia 48: 99-125.

LOWE, J.L. 1957. Polyporaceae of North America. The genus Fomes. State University, College of Forestry, Syracuse, New York.

LOWE, J.L. and R.L. GILBERTSON. 1961a. Synopsis of the Polyporaceae of the southeastern United States. J. Elisha Mitchell scient. Soc. 77: 43-61.

LOWE, J.L. and R.L. GILBERTSON. 1961b. Synopsis of the Polyporaceae of the western United States and Canada. Mycologia 53: 474-511.

MCKAY, H.H. 1959. Cultural basis for maintaining Polyporus cinnabarinus and Polyporus sanguineus as two distinct species. Mycologia 51: 465-473.

MOUNCE, I. and R. MACRAE, 1937. The behaviour of paired monosporous mycelia of Fomes roseus (Alb. and Schw. ex Fries) Cooke and Fomes cubroseus(Weir) Overh. Can. J. Res. 15: 154-161.

MURRILL, W.A. 1903. The Polyporaceae of North America. III. The genus Fomes. Bull. Torrey bot. Club 30: 225-232.

MURRILL, W.A. 1915. Western Polypores. W.A. Murrill, New York.

NEUHAUSER, K.S. and R.L. GILBERTSON. 1971. Some aspects of bipolar heterothallism in Fomes cajanderi. Mycologia 63: 722-735.

NEUMAN, J.J. 1914. The Polyporaceae of Wisconsin. Bibliotheca Mycologica, Bd. 32. Stecher Hafner Service Agency Inc., New York.

NOBLES, M.K. 1958a. A rapid test for extracellular oxidase in cultures of wood-inhabiting Hymenomycetes. Can. J. Bot. 36: 91-99.

NOBLES, M.K. 1958b. Cultural characters as a guide to the taxonomy and phylogeny of the Polyporaceae. Can. J. Bot. 36: 883-926.

NOBLES, M.K. 1965. Identification of cultures of wood-inhabiting Hymenomycetes. Can. J. Bot. 43: 1097-1139.

NOBLES, M.K. 1971. Cultural characters as a guide to the taxonomy of the Polyporaceae. In: Evolution in the Higher Basidiomycetes. Edited by: R. Peterson, University of Tennessee Press, Knoxville. pp. 169-196.

OVERHOLTS, L.O. 1953. The Polyporaceae of the United States, Alaska, and Canada. (Prepared for publication by J.L. Lowe), University of Michigan Press, Ann Arbor.

PEGLER, D.N. 1973. The polypores. Bull. Br. mycol. Soc. No. 7. 2nd ed.

PINTO-LOPEZ, J. 1952. Polyporaceae - contribucao rara a sua Bio-taxonomica. Mems Soc. broteriana 8: 5-214.

PLUNDETT, B. 1956. The influence of factors of the aeration complex and light upon fruit-body form in pure cultures of an agaric and a polypore. Ann. Bot. (London) 20: 563-585.

PURVIS, M.J., D.C. COLLIER and D. WALLS. 1966. Laboratory Techniques in Botany. Butterworth and Co. Ltd., London. 2nd. ed.

REA, C. 1922. British Basidiomycetae. A Handbook to the Higher British Fungi. Cambridge University Press, London.

ROBBERS, J.E., L.R. BRADY and V.E. TYLER. 1964. A chemical and chemotaxonomic evaluation of Inocybe species. Lloydia 27: 192-202.

SHIBATA, S., S. NATORI and S. UDAGAWA. 1964. List of Fungal Products. Chas. C. Thomas, Springfield, Illinois.

SHOPE, P.E. 1931. The Polyporaceae of Colorado. Ann. Mo. bot. Gdn 18: 287-456.

SINGER, R. 1963. The Agaricales in Modern Taxonomy. Cramer, Weinheim.

SMITH, A.H. 1966. The hyphal structure of the basidiocarp. In: The Fungi Vol. II. Edited by: G.C. Ainsworth and A.S. Sussman, Academic Press, New York. pp. 151-177.

SMITH, A.H. 1968. Speciation in higher fungi in relation to modern generic concepts. Mycologia 60: 742-755.

SNELL, W.H., W.G. HUTCHINSON and K.H.N. NEWTON. 1928. Temperature and moisture relations of Fomes roseus and Trametes subrosea. Mycologia 20: 276-291.

TALBOT, P.H.B. 1971. Principles of Fungal Taxonomy. Macmillan Press, London.

TEIXEIRA, A.R. 1960. Characteristics of the generative hyphae of polypores of North America, with special reference to the presence or absence of clamp connections. Mycologia 52: 30-39.

TEIXEIRA, A.R. 1962. The taxonomy of the Polyporaceae. Biol. Rev. 37: 51-81.

THOEN, D. 1970. Une nouvelle technique d'identification des Mycorrhizes ectotrophs par chromatographie sur couche mince. Revue mycol. 35: 258-264.

THOEN, D. 1975. Application de la chromatographie couche mince à l'étude des champignons mycorrhizateurs de Picea abies (L.) Karst. Bull. Jard. bot. natn. Belg. 45: 391-396.

TRAQUAIR, J.A. 1974. Biosystematic studies in the genus, Hirschioporus. Ph.D. thesis, University of Alberta, Edmonton.

TURNER, W.B. 1971. Fungal Metabolites. Academic Press, London.

TYLER, V.E. 1973. Chemotaxonomy in the Basidiomycetes. In: Evolution in the Higher Basidiomycetes. Edited by: R. Peterson, University of Tennessee Press, Knoxville. pp. 29-62.

VALADON, L.R.G. 1976. Carotenoids as additional taxonomic characters in fungi: a review. Trans, Brit. mycol. Soc. 67: 1-15.

VAN DER WESTHUIZEN, G.C.A. 1963. The cultural characters, structures of the fruit-body and type of interfertility of Cerrena unicolor. Can. J. Bot. 41: 1487-1499.

VON SCHRENK, H. 1900. Two diseases of red cedar caused by Polyporus juniperus n. sp. and Polyporus carneus Nees. Bull. Div. Veg. Physiol Path. U.S. Dep. Agric. 21.

WATSON, P. 1966. Investigation of pigments from Russula spp. by TLC. Trans. Brit. mycol. Soc. 49: 11-17.

WEIR, J.R. 1923. Fomes roseus (A. et S.) Cooke and Trametes subrosea nom. novum. Rhodora 25: 214-220.

WONG, W.M. 1973. The development of Fomes cajanderi Karst. in nature and in culture. M.Sc. thesis, University of Alberta, Edmonton.

YOKOYAMA, A., S. NATORI and K. AOSHIMA. 1975. Distribution of tetracyclic triterpenoids of lanostane group and sterols in higher fungi especially of the Polyporaceae and

related families. Phytochemistry 14: 487-497.

ZELLER, S.M. 1926. The brown-pocket heart rot of stone-fruit trees caused by Trametes subrosea Weir. J. agric. Res. 33: 687-693.

APPENDIX I

COLLECTIONS EXAMINED

Collections of Fomes roseus (Alb. & Schw. ex Fries) Cooke

Collection	Substratum	Location
ALTA 2505	Pinus	N. Mex.
2506	Picea	Alta.
2507	Picea	Alta.
2508	Picea	Alta.
2509	Picea	Alta.
2510***	--	--
2511	Picea	Alta.
2512	--	Alta.
2513	Pinus	Alta.
2514	Picea	Alta.
2515	Picea	Alta.
6899	Picea	Alta.
6900	Conifer	Alta.
6989	Picea	Alta.
6990	Picea	--
6991	Picea	Alta.
6992	Conifer	Alta.
6993	Conifer	--
6994	Picea	--

Collection	Substratum	Location
ALTA 2405	Conifer	Alta.
2406	Conifer	Alta.
2407	Spruce	Alta.
2408	Spruce	Alta.
2410	--	B.C.
2412	Spruce	Alta.
2413	Conifer	Minn.
2414	*Picea*	Alta.
2415	*Picea*	Alta.
2416	*Picea*	Alta.
2417	*Picea*	Alta.
2418	*Picea*	Alta.
2420	*Picea*	N.S.
3537	--	Alta.
3648	Conifer	Alta.
4162	--	Alta.
6169	*Picea*	Alta.
6193	*Pinus*	B.C.
6195	*Picea*	B.C.
6197	*Pinus*	B.C.
6251	*Pinus*	B.C.
6252	*Picea*	Alta.
6262	*Picea*	Alta.
6265	*Picea*	Alta.
6641	Conifer	--

Collection	Substratum	Location
ALTA 6646	*Picea*	Alta.
6647	Conifer	Alta.
6649	*Picea*	Alta.
6651	*Picea*	Alta.
6652	*Pinus*	Alta.
6654	*Picea*	B.C.
6655	*Picea*	B.C.
6661	*Picea*	Alta.
6662	*Picea*	Alta.
6667	*Picea*	Alta.
7062	*Picea*	Alta.
7063	*Populus*	Alta.
7064	*Pinus*	Alta.
7065	*Picea*	Alta.
7066	Conifer	Alta.
7068	*Picea*	B.C.
CFB 3567	*Picea*	Alta.
3627	*Picea*	Alta.
3634	*Picea*	Alta.
3655	*Picea*	Alta.
3932	*Picea*	N.W.T.
4086	*Picea*	Que.
4350	*Larix*	Alta.
4426	*Pinus*	Alta.
4665	*Picea*	N.W.T.

Collection		Substratum	Location
CFB	11720	Conifer	N. Mex.
TRTC	--*	*Abies*	N.E. U.S.A.
	--*	Conifer	N.Y.
	--*	--	N.Y.
	203	Conifer	Idaho
	256	*Picea*	Ont.
	1030	*Picea*	Ont.
	1090	*Picea*	Ont.
	4272*	*Pinus*	Tenn.
	4273*	*Pinus*	Tenn.
	6308	Conifer	Ont.
	6764	*Picea*	Ont.
	18587	*Picea*	Ont.
	18589*	*Pinus*	Ont.
	10311	*Pinus*	Ont.
	10312*	*Picea*	Ont.
	47997	*Picea*	Ont.
	F.P.45608*	*Picea*	N.H.
	--	*Picea*	Czech.
	--*	*Picea*	Russ.
DAOM	1404	*Picea*	Ont.
	1449	*Picea*	Ont.
	2355	*Picea*	Que.
	8154	*Picea*	Que.
	9114	*Picea*	Que.

Collection	Substratum	Location
DAOM 17572**	Picea	Alta.
30840	Picea	B.C.
F2202*	Picea	N.S.
RC 104	Picea	Alta.
106	Picea	Alta.
159	Picea	Alta.
160	Picea	Alta.
161	Picea	Alta.
163	Picea	Alta.
170	Picea	Alta.

Collections of Fomes cajanderi Karst.

Collection	Substratum	Location
ALTA 2388	Pinus	Alta.
2389	Conifer	Alta.
2390	Picea	Alta.
2391	Pinus	Alta.
2392	Pinus	Alta.
2395	Pinus	Alta.
2396	Picea	Alta.
2397	Picea	Alta.
2401	Pinus	Alta.
2402	Picea	Alta.
2403	Pinus	Alta.

Collection	Substratum	Location
ALTA 6995	*Populus*	--
6996	Conifer	Alta.
6997	--	--
6998	*Picea*	--
7021	Conifer	Alta.
7022	*Picea*	Alta.
7023	*Picea*	--
7024	*Picea*	Alta.
7025	*Picea*	--
7026	*Picea*	Alta.
7027	*Picea*	Alta.
7028	Conifer	Alta.
7029	Conifer	--
7030	*Populus*	Alta.
7031	--	--
7032	*Picea*	--
7033	*Picea*	B.C.
7034	Conifer	Alta.
7035	*Picea*	B.C.
7036	*Picea*	Alta.
7088	--	Alta.
7094	*Picea*	Alta.
7111	*Picea*	Alta.
7112	*Picea*	--
7117	*Picea*	Alta.

Collection	Substratum	Location
CFB 4813	*Pinus*	Alta.
4946	Conifer	Alta.
5129	*Picea*	Alta.
5184	*Picea*	Alta.
5375	*Picea*	Alta.
5381	Charcoal	Alta.
5389	*Picea*	N.W.T.
5399	*Picea*	N.W.T.
5413	*Picea*	Alta.
5414*	*Picea*	N.W.T.
5424	*Pinus*	Alta.
5434	*Picea*	Alta.
5982	*Picea*	Alta.
6010	*Picea*	N.W.T.
6160	*Picea*	Alta.
6645	*Pseudotsuga*	B.C.
7345	*Picea*	N.W.T.
7382	*Pinus*	Alta.
7446	*Pinus*	N.W.T.
8179*	*Picea*	N.W.T.
8199*	*Picea*	N.W.T.
8941	*Picea*	Alta.
20536	*Picea*	Que.
20537	*Picea*	B.C.
20538	*Pseudotsuga*	B.C.
	Pseudotsuga	

Collection		Substratum	Location
CFB	DACFP 33	Picea	Alta.
	DACFP 109	Picea	Alta.
	DACFP 155	Picea	Alta.
	DACFP 200	Pinus	Alta.
	DACFP 221	Conifer	Alta.
	DACFP 1004*	Picea	Alta.
	DACFP 1758	Larix	B.C.
TRTC	33171	Pinus	Alta.
	33172	Picea	Ont.
	33174	Picea	Ont.
	33178	Pinus	Ont.
	33179	Picea	Ont.
	33181	Pinus	Ont.
	33182	Picea	Ont.
	33183	Picea	Ont.
	33184	Picea	Ont.
DAOM	1639	Pseudotsuga	Oreg.
	F2378	Pseudotsuga	B.C.
	17529	Picea	Man.
	31505	Picea	N.B.
	31513	Pinus	N.B.
	31855	Picea	N.W.T.
	53725	Picea	N.S.
	145624	Prunus	Ont.

Collection		Substratum	Location
DAOM	146506	Pinus	Ariz.
RC	3	Picea	Alta.
	14	Picea	Alta.
	83	Picea	Alta.
	105	Picea	Alta.
	107	Picea	Alta.
	123	Railroad tie	Alta.
	128	Picea	Alta.
	162	Picea	Alta.
	168	Picea	Alta.
	216	Picea	Alta.

* -alternate species

** -mixed collection

*** -neither species

APPENDIX II

Collections of *Fomes roseus* (Alb. & Schw. *ex* Fries) Cooke and *Fomes cajanderi* Karst. examined from various substrata

	ALTA	CFB	TRTC	DAOM	RC
Fomes roseus					
Larix	0	1	0	0	0
Picea	23	3	8	8	7
Pinus	2	0	1	0	0
Populus	2	0	0	0	0
Unidentified Conifer	11	0	2	0	0
Fomes cajanderi					
Abies	0	0	1	0	0
Larix	0	1	0	0	0
Picea	26	23	7	3	9
Pinus	11	8	9	2	0
Populus	1	0	0	0	0
Prunus	0	0	0	1	0
Pseudotsuga	0	3	0	2	0
Unidentified Conifer	11	2	2	0	1

Appendix III. A developed, thin layer chromatograph of ethyl acetate soluble cyclic compounds from the basidiocarps of five wood-rotting fungi.
Three separate benzotropolones and two non-separated phenolics are shown.

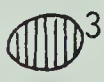
Solvent - Acetone:benzene; 1:4
Developing agents - 1% Vanillin:H_2SO_4; 4:1, followed by gentle heat

Legend

Sf	solvent front
O	origin
Fr	Fomes roseus (Alb. & Schw. ex Fries) Cooke
Fc	Fomes cajanderi Karst.
Fpi	Fomes pini (Thore ex Fries) Karst.
Fpa	Fomes pinicola (Swartz ex Fries) Cooke
Ff	Fomes fomentarius (L. ex Fries) Kickx

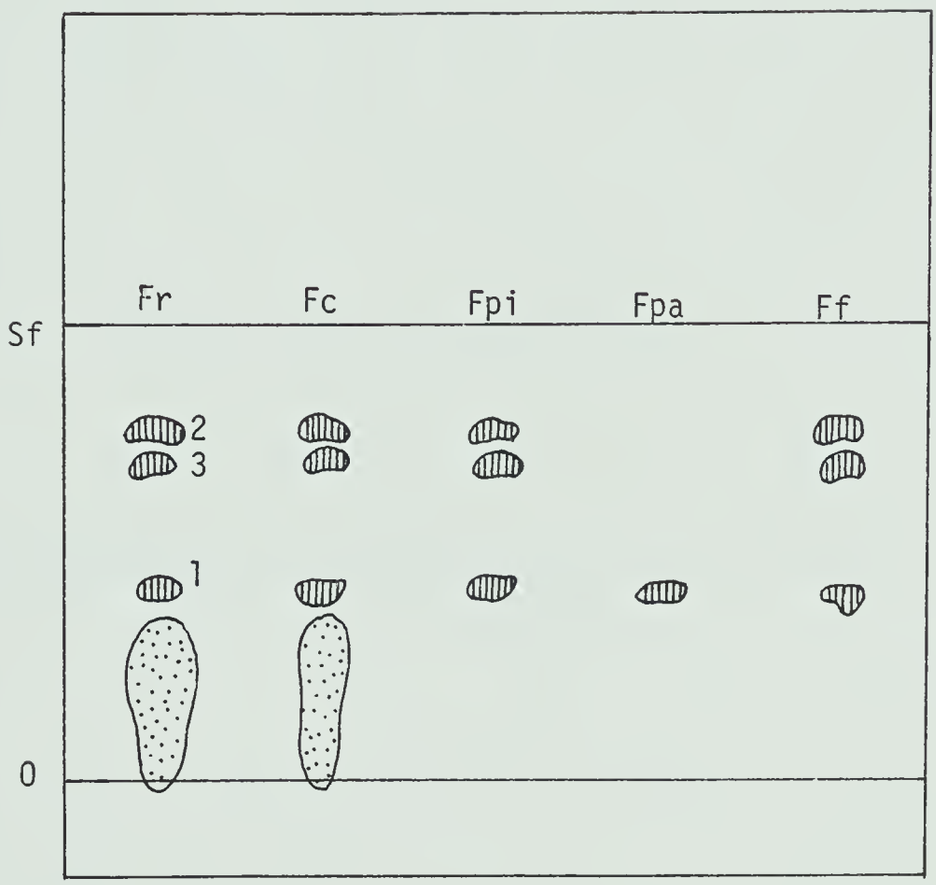
Benzotropolone I

Benzotropolone II



Benzotropolone III


Phenolics I and II

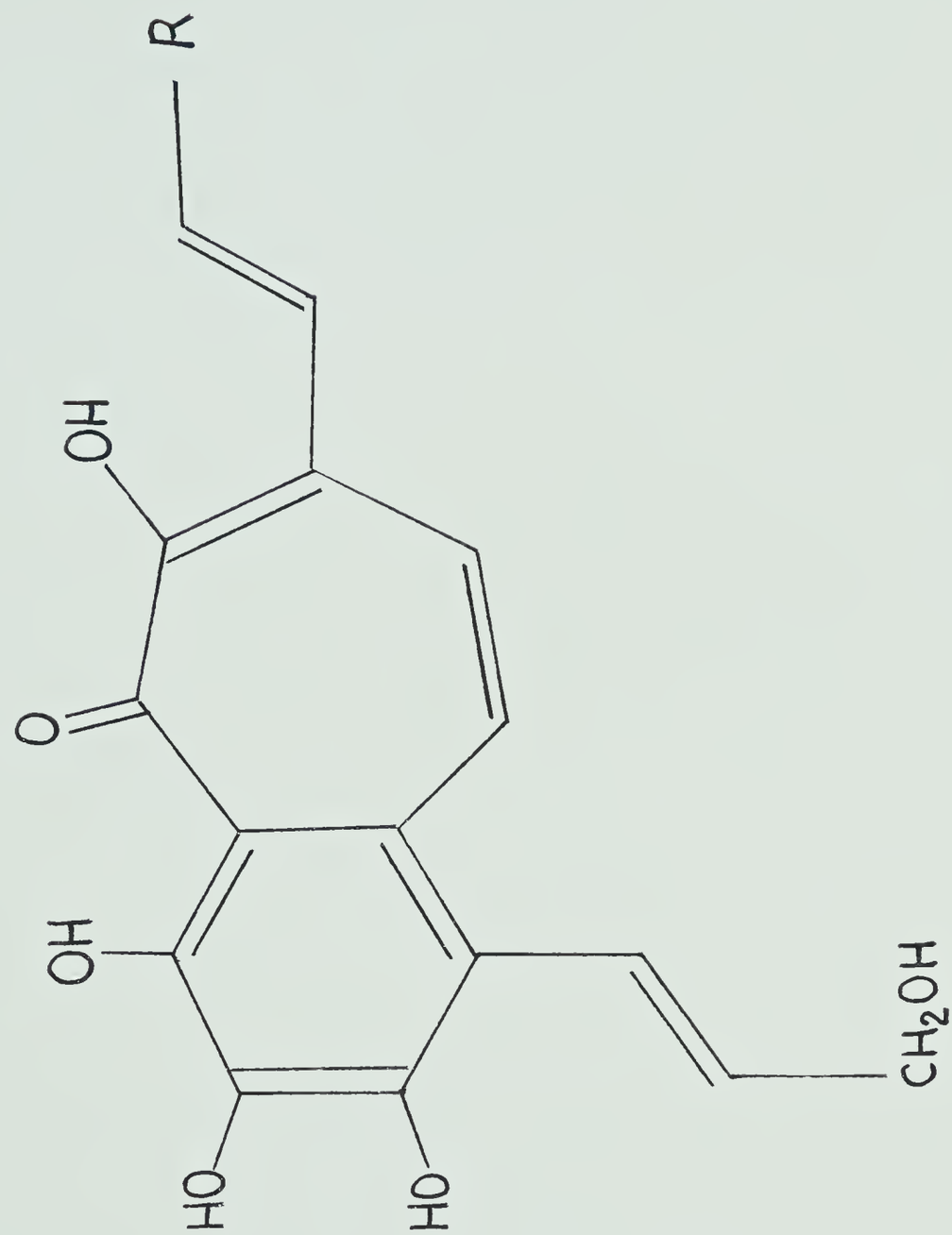

Fr
Fc
Fpi
Fpa
Ff
Sf
2
3
1
0

Appendix IV. UV spectrographs of benzotropolone I and phenol I isolated from Fomes roseus (Alb. & Schw. ex Fries) Cooke

Phenol I
Concentration Coefficient
210
222
254
λ(nm)

Benzotropolone I
Concentration Coefficient
208
274
330
λ(nm)

Appendix V. Benzotropolone structure
R:CH_2OH - 'Fomentariol'


R
OH
O
OH
HO
HO
CH2OH